THE BEHAVIOUR AND SOCIAL ORGANISATION OF THE BRUSH-TAIL POSSUM (*TRICHOSURUS VULPECULA*: KERR)

by

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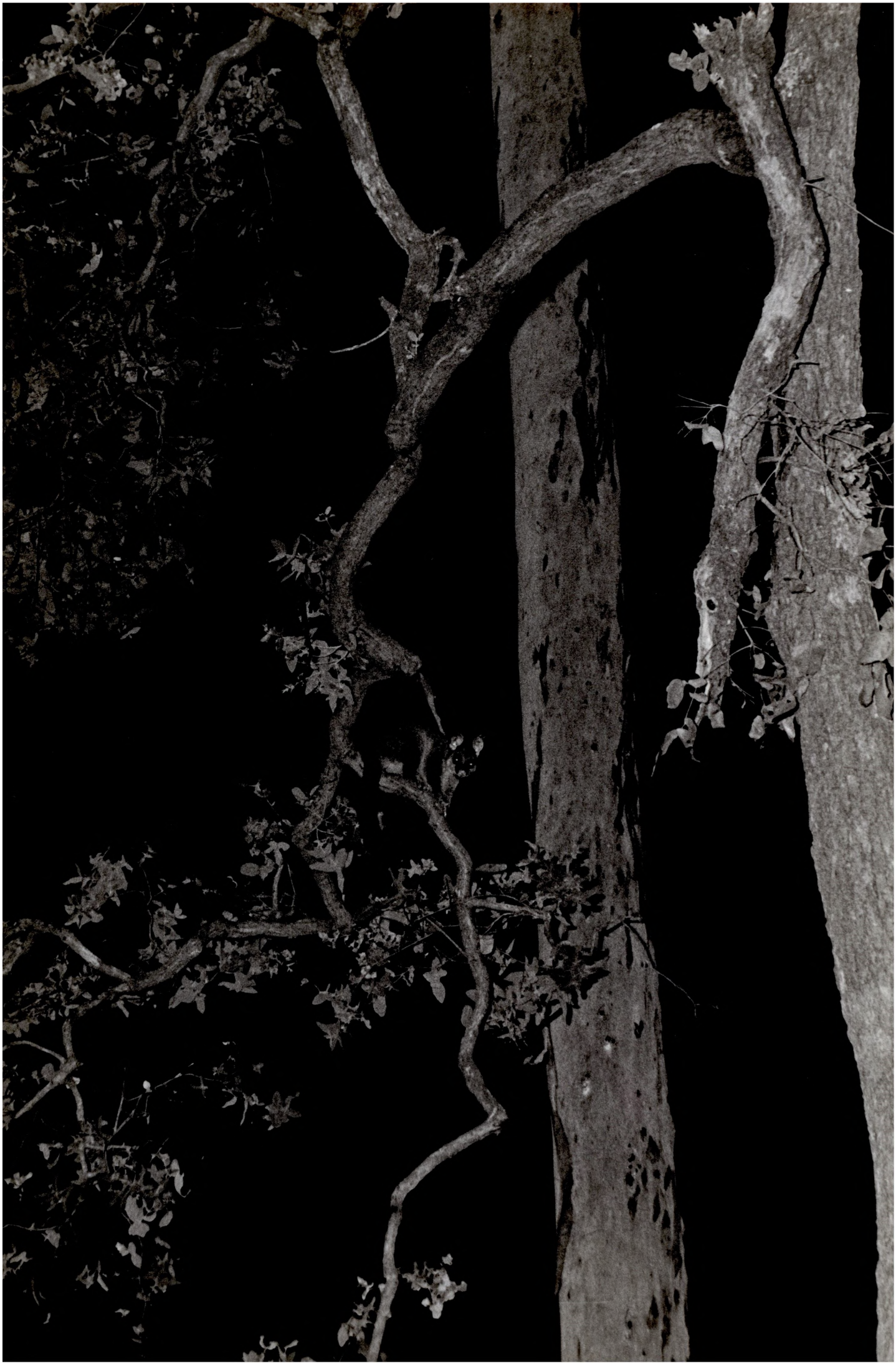
A thesis submitted for the degree of Doctor of Philosophy within the University of Queensland.



Trichosurus vulpecula (Kerr 1792)

ABSTRACT

The primary aim was to examine the social organisation of the brush-tail possum (Trichosurus vulpecula) in a modified open forest habitat near Brisbane.

On the 17 ha study area densities over three years remained stable at 2.14, 2.19, and 2.14/ha. There was a pronounced autumn breeding season, and 22% of the females bred twice a year. Mature eucalypt leaves were the staple diet. Time of emergence from dens at dusk was the same for males and females with little variation, but at dawn males returned significantly later than females. Possums spend about 1/3 of the night sitting and 25% of it feeding in trees. Males spend twice as much time on the ground as females, and both sexes spent little time on social interactions.

An auditory repertoire of 22 sounds, 19 of them social, is described. Two graded series formed a group of agonistic calls, with emancipation of one as an alarm call. More discrete calls are given by distressed young, and an appeasement call very similar to the juvenile distress call is given by the courting male. Buccal clicks given during stressful interactions may have a social function. The significance of the unique dilated thyroid cartilage functioning as a possible resonator is discussed.

Scent marking by chinning and chesting took place in the vicinity of, or at a place visited by another possum, and its function is considered to be the transfer of information concerning the locality and status of the marking individual. Little urine marking was observed, but its function is possibly similar to chinning and chesting. It is suggested that secretion from the paracloacal scent gland acts as a submissive signal.

An individual distance of 1m between male and female is maintained by female aggression. Following a consort period of 30-40 days males and females may act as contact animals and mate without aggression, but mating which occurs without a consort period is aggressive and may attract other males. Adult females are dominant to males, except that the

slightly larger size of males may allow them to win an interaction when sufficiently motivated. Interactions between adult males occur most frequently near an oestrous female. Absolute ranking positively correlated with age and/or size exists between males, and primary and secondary consort males may accompany a female. Interactions between females were rare, but a ranking system similar to that of males probably existed.

Territorial behaviour was based on mutual avoidance of co-dominants, and defence of an area was restricted to a den tree.

Young emerge from the pouch at the age of 4½ to 5 months, and a contact relationship with the mother continues until 8-9 months old. The joey is mainly responsible for maintaining proximity to its mother, although she will wait if separated and return to her joey if it is distressed. At 8-9 months the relationship ceases to be a contact one away from the den, as a result of increased aggression by the female, which includes olfactory marking. At the den cohesive and contact behaviour continues until the juvenile becomes independent at 9-16 months. Interactions between dependent juveniles were not observed, and between older juveniles were rare. Play was rudimentary, only occurred between mother and joey, and was agonistic in nature.

Dispersion is centred on dens, and 89.5% of observations were of a single adult using a den. Male and female home ranges are superimposed independently of each other. Males had larger home ranges, travelled further each night, and changed dens more frequently than females.

Between individuals of the same sex and status exclusive areas existed, but males may penetrate the exclusive areas of others when converging on a female. The exclusive areas of high status males and females were completely overlapped by lower status individuals. Males achieved exclusive areas by about the end of their fourth year and females a year earlier. Juvenile females established home ranges in, or adjacent to, the maternal home range, while young males dispersed between the ages of 9 and 16 months.

Social behaviour is compared with that of other arboreal marsupials,

and the ecological significance of its social organisation discussed.

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Statement of Sources

All the work described in this thesis is original and my own, except where noted in the acknowledgments and specifically stated in the text. The material presented has not been submitted for another degree in the University of Queensland or elsewhere.

J.W. Winter

J.W. Winter.

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CHAPTER I

INTRODUCTION

1.1 Preamble

The social organisation of an animal depends not only on the social interactions between individuals, but also on the interaction with other features of the environment such as food, shelter, and predators, which produces a characteristic pattern of dispersion for the species. An appreciation of the importance of the environment has meant that many studies of social organisation have been made in the field on natural populations, particularly as the use of captive animals can lead to significant distortions of behaviour (see Kaufmann and Kaufmann 1963, Rowell 1967, and Leyhausen 1965). This in turn has meant that most studies on mammalian social organisation have been on the conspicuous and larger diurnal species such as ungulates, primates, large carnivores, and pinnipeds. Not only are most of these studies concentrated on gregarious animals but an initial interest by workers into the behavioural mechanisms of group cohesion and the study of primates as a means of gaining insight into the evolution of man's behaviour has meant a selection of so called "social" as opposed to "solitary" species as study subjects. Even among the smaller mammals it has been the gregarious or colonial species which have received most attention, for example coatis (Kaufmann 1962), prairie dogs (King 1955), the European rabbit e.g. (Southern 1948, Mykytowycz 1961, 1965, Myers and Poole 1963), and two diurnal gregarious lemurs (Jolly 1966). Solitary species have received little attention partly because few diurnal species appear to be solitary and those that are, are relatively inconspicuous. Tree squirrels and chipmunks, groups which represent small diurnal mammals with individual home ranges or territories and which are conspicuous because of their activity and vocalis ations, have received the most attention. However, as Leyhausen (1965) points out, with solitary species attention has been focussed on agonistic behaviour. Thus although there are numerous studies on territoriality and hierarchy in squirrels and chipmunks (e.g. Martinsen 1968, Taylor

1966, Wolfe 1966, Smith 1968 and Dunford 1970) there is no comprehensive field study of their social organisation, the closest being that of Smith's (1968) on the genus Tamiasciurus. Other studies on solitary species have tended to emphasis general ecology such as that of Calaby's (1960) on the marsupial ant-eater, Myrmecobius.

Of the large number of nocturnal mammals most of what is known of their social organisation is inferred from indirect methods such as trapping, and various methods have been devised for measuring home ranges, territories, activity centres etc. from the trapping data (see Jewell 1966, and Brown 1966 for reviews). However, very little is known about the behavioural mechanisms which maintain a given spacing of individuals. A species is usually assumed to be territorial, if trapping indicates an exclusive area, particularly if individuals show pronounced agonistic behaviour to one another, and scent mark. Baran and Glickman's (1970) demonstration that scent marking is not necessarily territorial comes as a very timely caution.

Initial studies on solitary mammals indicate a diversity of social organisation. For example the home range of a dominant Apodemus may completely overlap the home ranges of several subordinates (Brown 1966); Felis catus have a "brotherhood" of more or less equal status individuals (Leyhausen 1965); two nocturnal prosimian studies (Microcebus murinus, Martin 1972, and Galago demidovii, Charles-Dominique 1972) have population foci with central and peripheral males; the marsupial ant-eater (Calaby 1960) has very widely spaced individuals; and there is the classical overlapping home range and defended territory of the snipmark (Dunford 1970) and the highly territorial Tamiasciurus (Smith 1968).

The term 'solitary' should not be taken to imply a dichotomy of mammalian social organisation between 'solitary' on the one hand and 'social' or gregarious on the other, but a continuum from the most gregarious at one end to the most solitary at the other. Thus a lack of basic field studies on mammals towards the solitary end of the continuum is not only a gap in our knowledge of the diversity and function of social

organisation of solitary mammals, but also a serious lack of understanding of mammalian social systems as a whole.

1.2 Aims

The principal aim of this thesis is to determine the role of behaviour in maintaining the social organisation of a "solitary" mammalian species. Emphasis is on the descriptive analysis of field behaviour as a basis to generate hypotheses.

The study animal chosen is a nocturnal marsupial, the brush-tail possum (Trichosurus vulpecula (Kerr 1972), belonging to the family Phalangeridae (following Kirsch 1968), is a folivore with a wide range of habitats, but predominantly a denizen of open eucalypt forest. It was chosen because it is common in the Brisbane district and relatively easy to observe in the eucalypt trees. Another advantage of studying the brush-tail possum is that its basic biology is well known and a number of trapping studies have been made of it both in Australia and New Zealand.

1.3 Review of Trichosurus vulpecula Biology

Trichosurus vulpecula has been a popular animal to work on because it is easy to capture and to keep in the laboratory (Bolliger 1940), and it was introduced into New Zealand to establish a fur trade (Pracy 1962) but has since become a pest (Wodzicki 1950, Tyndale-Biscoe 1960, Pracy and Kean 1969). A review of the biology relevant to the present study follows.

Reproductive biology of the brush-tail has been thoroughly studied. The female is polyoestrous and monovular with the oestrous cycle varying in length from 22 to 32 days during the main breeding seasons of autumn and spring, but with some being as long as 58 days during the winter, and with most females going into anoestrous during the summer (Pilton and Sharman 1962, Kean Marryatt and Carroll 1964). Oestrus lasts for 2-3 days with ovulation occurring 1 day after copulation according to Kean, Marryatt, and Carroll (1964), or up to 3 days after oestrus according to Pilton and Sharman (1962). A copious vaginal mucus is secreted for a period of 3-4 days from commencement of oestrus until about half a day

after ovulation (Hughes and Rodger 1971). The Gestation period is about 17.5 days (Lyne, Pilton and Sharman 1959, Pilton and Sharman 1962) followed by a five month period of nursing in the pouch and then a further 2 months when the young is dependent on its mother outside the pouch (Dunnett 1956, 1964). Lactation is initiated and maintained by the suckling stimulus (Sharman 1962). Births tend to follow a seasonal pattern of a pronounced peak in autumn (March-April-May), a subsidiary peak in spring (September-October) with some breeding during the winter, but virtually none in summer (Bolliger 1940, Dunnett 1956, 1964, Gilmore 1969, Smith, Brown and Frith 1969, Crawley 1973). The relative size of the two breeding peaks varies with the spring peak being relatively small to absent in New Zealand (Gilmour 1969, Crawley 1973) and New South Wales (Smith et.al. loc. cit.), whereas at Canberra the spring peak is relatively larger with little winter breeding, (Dunnett 1964). The only significant departure from this pattern was described by Pilton and Sharman (1962) for the Adelaide area, where the autumn peak was followed by a gradual decline to the beginning of summer with no winter trough or spring peak. There was, however, the usual lack of summer breeding. One young is born and raised at a time and twins are rare (Wodzicki 1950, Pilton and Sharman 1962, Kean 1971, Crawley 1973). Females are capable of breeding twice a year and at Canberra about half the females did so (Dunnett 1964). However, the proportion of females breeding twice a year may vary considerably as Kean (1971) records only one double breeder from 8,000 females examined and suggests that it may be a function of population density and food. Young females are capable of breeding by the end of their first year (Jones 1921, Wodzicki 1950, Kean, Marryatt and Carroll 1964, Gilmore 1969, Smith, Brown and Frith 1969), but Kean (1959) considered that they did not successfully rear their first young until they are in their third year especially when in a stable population, and Crawley (1973) records females as old as 4 years as not having bred.

Males produce motile sperm throughout the year (Bolliger and Carrodus

1938, Belliger 1940, 1942). Kean (1959) suggested endogenous fluctuations of sperm production with the lowest incidence in summer, and Gilmore (1969) presents some evidence for this. Prostate weight shows a marked seasonal fluctuation (Gilmour 1969) which closely correlates with the seasonal pattern of births. Thus there is evidence that the male goes through a seasonal sexual cycle, but one which is not characterised by a marked regression of the testes or of a complete stop in sperm production. Males reach sexual maturity a little later than females and probably not until they are at least 18 months old (Gilmore 1969).

Diet of the brush-tail has not been examined carefully in Australia, but it is known to be mainly vegetarian (Troughton 1962), and Owen and Thomson (1965) report that it consists chiefly of the mature foliage of Eucalyptus trees, as well as a narrow range of indigenous and introduced shrubs and trees. It is not however, a specialised eucalypt feeder and it will take a wide range of vegetable food, emphasised by its successful introduction into New Zealand. There its diet consists of a wide range of foliage, flowers and fruit of indigenous trees (Mason 1958, Gilmore 1967) and in pastoral areas a high porportion of grass and clover (Gilmore 1965, 1967, Harvie 1973). Also in Australia the brush-tail has taken to stripping the bark from exotic Pinus sp. in order to scrape away the cambial layer with their incisors (McNally 1955). Items of animal food are rarely taken and in the case of insects may be fortuitous (Mason 1955). However, as Gilmore (1967) points out the brush-tail is an opportunist feeder and will eat a wide range of food scraps around human habitations, and he reports some observations made by Pracy of possums feeding on camp meat, deer carcasses and other dead possums during a population peak in a depleted habitat. There is also one report of a "grey possum", presumably Trichosurus vulpecula, killing domestic chickens (Anon 1935).

At Canberra, Australia, an overall population density of approximately 0.43 possums/ha has been recorded (extracted from Dunnett 1964). In New Zealand, however, much higher densities are reported, an average of

5.7/acre (14/ha) and suggested extreme densities of 12/acre (30/ha) were recorded in one study (Batcheler, Darwin and Pracy 1967), and in another at Crongorongo densities ranging from 10.6/ha to 6.4/ha (Crawley 1973). These high densities may represent an initial population explosion characteristic of a successfully introduced animal (Elton 1958), but in the area where densities of 6.4 to 10.6/ha were recorded brush-tail possums had been established for approximately 70 years (Crawley 1973).

Males have larger home ranges than females (Dunnett 1956, 1964, and Crawley 1973) ranging in size from 4.9-10.3 acres (1.96-4.12 ha) in the Canberra population to a mean of 0.8±0.05 ha in the much denser Orongorongo population. Female home ranges ranged in size from 0.62 acre (0.25/ha) to 5.97 acres (2.39 ha) at Canberra, to 0.46±0.04 at Orongorongo. In another New Zealand study Jolly (1973) found average home range areas of 0.8ha for males and 0.3ha for females. Movements of 300 to 400m have been recorded (Tyndale-Biscoe 1955, Jolly 1973) Kean (reported in Gilmore 1967) is of the opinion that brush-tail possums will move up to 3.5km in a night.

Natural life spans of up to 12 years have been recorded in New Zealand (Crawley 1970) and of 6 years at Canberra (MacLean 1967), but little is known about age composition of a population. On the basis of epiphyseal union Tyndale-Biscoe (1960) reports that from one sample taken from a stable population 80% were over 2 years old, and suggests a rough figure of 5-6 years as the average life expectancy.

Dunnett (1964) concluded at the end of two capture release studies of the brush-tailed possum at Canberra, Australia, that:-

"The evidence, both natural and experimental shows clearly that adult males are mutually exclusive and in general defend territories which are much larger than the undefended overlapping individual ranges of adult females.....In some situations....a dominant subordinate relationship may exist between adult males who are not completely mutually exclusive. Males may occupy the same territory for several years.... Young males are tolerated in the territories until they are about a year

old, but when they begin to mature, they are apparently driven out and seek to establish a territory of their own. There is also good evidence of the presence of transient adult , as well as young, males moving through the study areas apparently in search of vacant territories. Several cases are known of such animals settling down in vacant territories...

Breeding females are also resident and sedentary but in areas where they are numerous they do not defend their individual ranges from other females. In the unnatural area ... a very great amount of overlap occurs in the homestead area, but in semi-natural situations numbers are usually smaller and overlap consequently less, though it does occur .... Young females settle to breed in their native area quite frequently, and there is no very good evidence, for transient females, either young or old.

It is clear that the number of males is limited as a result of their territorial behaviour, but the number of females does not appear to be affected by social factors. The number of females per male territory varies from ten to eleven in the territory of [2] to one or two in most cases. Clearly the ... homestead is exceptional in supporting so many females, but the factors which permit the population to build up to such a level are unknown. Cover is certainly more abundant there, but food does not appear to be conspicuously more plentiful than in some of the areas of natural woodland ...."

In the denser population of Orongorongo Crawley (1973) concluded that no part of an individual's home range was exclusive, and that territorial behaviour was not conspicuous. A change in the pattern of survivorship during control operations suggests that territorial behaviour may break down at densities of about 5/acre (12 /ha)(Batcheler, Darwin and Pracy 1967).

There are two general studies of the behaviour of the brush-tailed possum, but both were based on captive animals and are of a preliminary nature (Jones 1921, and Kean 1967). The possum possesses a number of scent glands (Bolliger and Hardy 1944, Bolliger and Whitten 1948), and some preliminary cage experiments have been done on the response of both species

of Trichosurus to the secretion from these glands (Thomson and Peers 1962). These studies give a good preliminary account of the behavioural repetoire of the brush-tail (discussed in detail in following chapters), but give little indication as to how the behaviour is used in the field to maintain the animals social organisation, apart from inferences made from the occasional field observation.

Figure 2.1: Aerial photograph of the study area (within dotted line) at Moggill Farm.

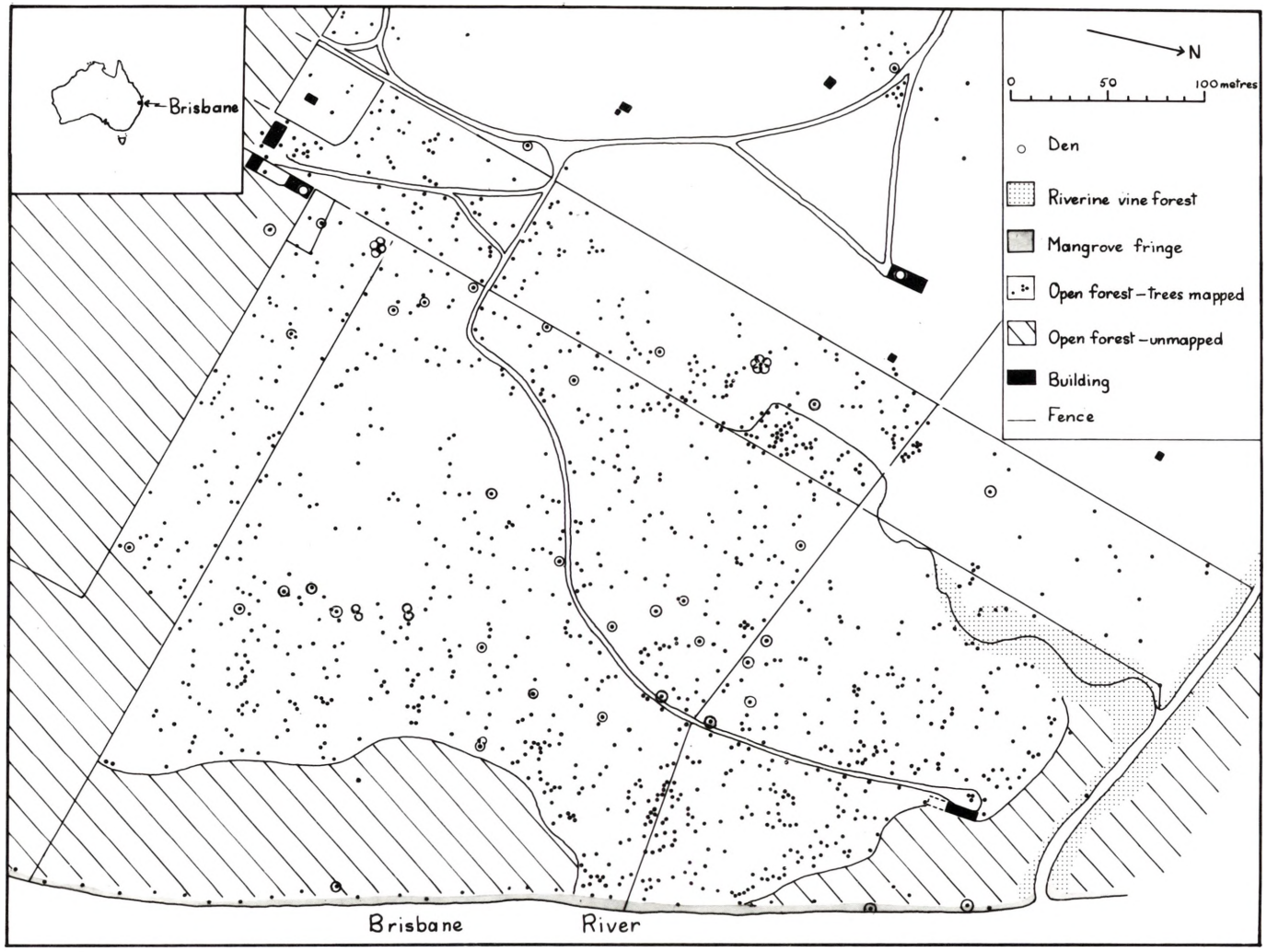


Figure 2.2: Map of study area at Moggill Farm.

Figure 2.3: Grassy open forest at Moggill Farm typical of much of the study area.

Figure 2.4: Mangrove fringe and continuous canopy of Eucalyptus terreticornis along the banks of the Brisbane River at Moggill Farm

CHAPTER 2

STUDY AREA AND METHODS

2.1 STUDY AREA

The study area was on the University of Queensland Veterinary Farm, Moggill (Latitude 27°32'50"S, Longitude 152°53'50"E) about 13 Km W.S.W. of Brisbane. The 17 hectare site was on relatively flat ground on the north bank of the Brisbane River which is still tidal in this region (Figs. 2.1 and 2.2).

Originally the area was probably 'Shrubby Open Forest' (Leeper 1970) with eucalypts as the main canopy trees. It has since been modified for cattle grazing by removing the shrub layer and thinning the trees to give a 'Grassy Open Forest' (Leeper 1970) with a canopy height of 20 to 30m (Fig. 2.3). To the west a 150-200m strip of open ground formed an effective, though not complete, barrier to possum movements, and to the east the 100-200m wide Brisbane River formed a complete boundary. Southwards the area was continuous with similar habitat, and to the north the boundary was marked by a tidal creek beyond which the density of trees dropped away markedly.

Three eucalypts were the most common tree in the area - Forest Red Gum (Eucalyptus territicornis), Gum topped Box (E.hemiphloia), and narrow leaved iron-bark (E.crebra). The iron-barks were distributed throughout the area except within about 100m of the river, whereas the other two species tended to be restricted to certain areas, the gum topped boxes on the stonier ridges to the south and west, and the forest red gum to the east on the deeper soil especially along the river bank where they formed a continuous canopy. Moreton Bay Ashes (E.tesselaris) and spotted gums (E.maculata) also occurred as scattered trees. Other trees with an open canopy similar to that of the eucalypts were also present in relatively low numbers - Angophora subvelutina, Tristania suaveolens, Acacia aulacocarpa, and Casuarina cunninghamiana. A mangrove fringe, 2-3m wide, of Avicennia marina var. australasica and Aegiceras corniculatus occurred along the river bank under the forest red gums (Fig. 2.4). Along the creek to the north a 10-15m wide strip of riverine

Figure 2.5: A brush-tail possum in the canopy of a eucalypt tree. Note the open nature of the canopy.

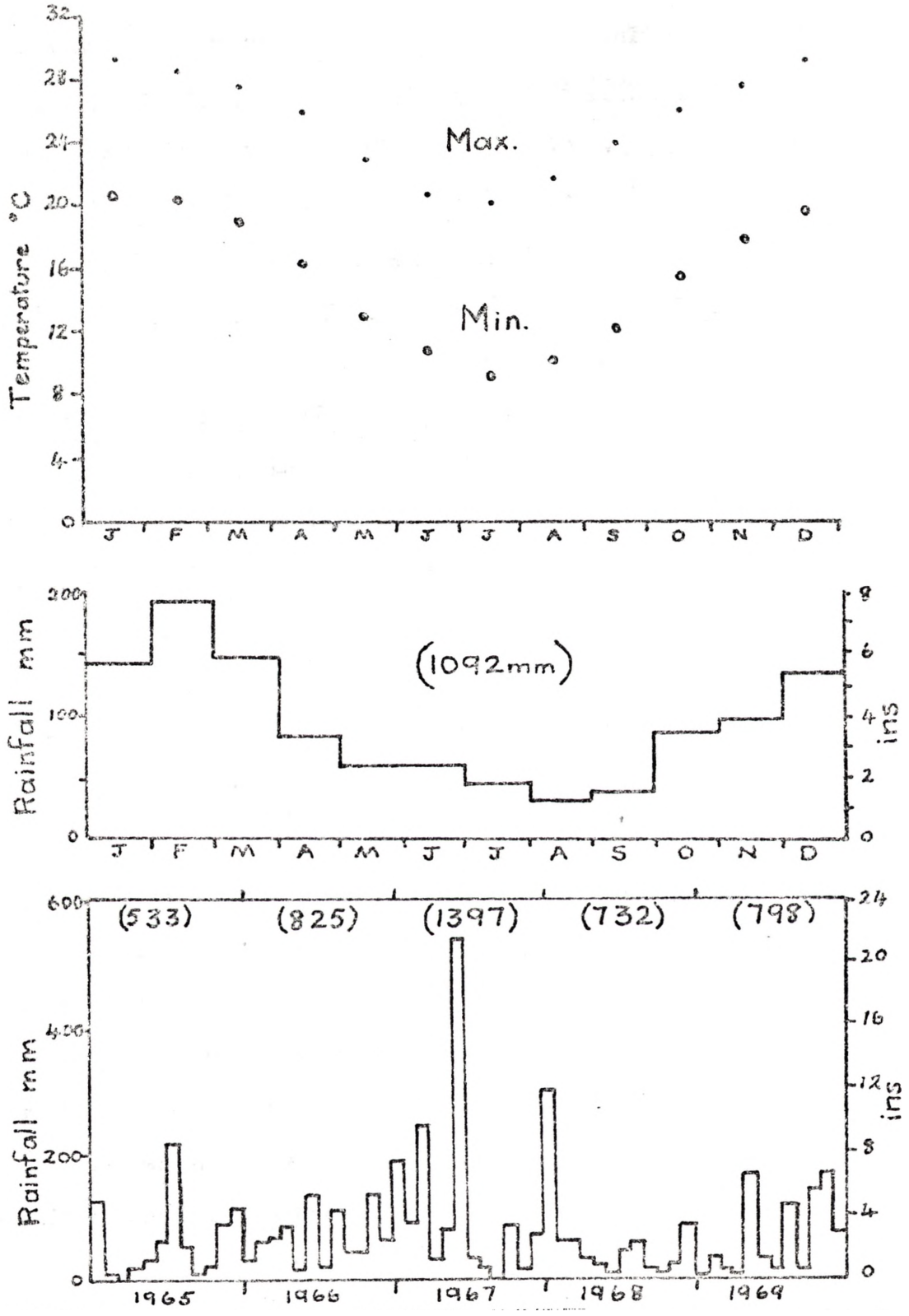


Figure 2.6: Top - 85 year mean monthly temperatures for Brisbane (supplied by the Bureau of Meteorology).

Middle - 30 year mean monthly rainfall for Brisbane (Queensland Year Book 1969 & 1970).

Bottom - Monthly rainfall at Moggill Farm during study period (supplied by Veterinary School, University of Queensland).

vine forest formed a continuous canopy of dense foliage and a few scattered trees such as Aphananthe philippinensis, Mallotus philippinensis, Melia azedarach var. australasica, and Euroshinus falcatus extended into the main part of the study area. The ground layer under the eucalypts consisted mostly of exotic grasses e.g. Cynodon dactylon, Eragrostis tenuifolia, Panicum decomposition and herbs e.g. Sida rhombifolia, Ageratum houstonianum, Salvia coccinea, and Malvastrum coromandelianum.

Continuous observations on a possum were made possible by (1) the open canopy of the eucalypt trees (Fig. 2.5), (2) the non-contiguous crowns of the trees which meant that to move from one tree to another a possum had to come down to the ground, and (3) the shortness of the grass due to cattle grazing, except in the exceptionally wet year of 1967 when the grass was rank.

Brisbane has subtropical temperatures (Fig. 2.6) with the occasional frost in winter. Winters tend to be drier than summers but rainfall from year to year can be very erratic with heavy falls in winter (Fig. 2.6).

The study area was mapped on a plane table using a scale of 40ft. = 1cm. All major trees, except in the region of dense tree cover along the river bank and creek, were plotted on the map and numbered with an aluminium garden tag. Along the river bank and creek only sufficient trees to act as markers were actually plotted and numbered. To test the accuracy of the mapping a line 630m long was measured from tree to tree both on the map and on the ground with an average error of 1.34m (S.E.0.21m, n=20) on distances ranging between 19.5 and 50.3m, and a total accumlative error of 0.61m over the full distance (Table 2.1).

Table 2.1

Distances between a consecutive series of trees measured on the ground and on the map as an indication of the degree of error in mapping the area.

Distance between trees (ft.) as measured on the:-			
ground	map	difference	Accumulative difference
64	65	+1	+1
71	69	-2	-1
81	85	+4	+3
87	95	+8	+11
75	67	-8	+3
92	90	-2	+1

	Ground	map	Difference	Accumulative difference
cont.	78	70	-8	-7
	114	121	+7	0
	93	82	-11	-11
	150	150	0	-11
	142	143	+1	-10
	125	130	+5	-5
	66	63	-3	-8
	71	75	+4	-4
	145	142	-3	-7
	98	100	+2	-5
	100	105	+5	0
	112	120	+8	+8
	165	165	0	+8
	138	132	-6	+2
Total	2067 (630m)	2069 (631m)	+2 (0.61m)	+2 (0.61m)

mean = 4.4±0.69ft(1.34±0.21m),S.D.=3.07ft(0.94m)

2.2 METHODS

2.21 Techniques of Direct Observation

The basic method used throughout the study was the direct observation of a field population with the aid of a spotlight and binoculars. To clarify the limitations of this method, such as the effect of the spotlight on behaviour, and to indicate the extent to which these have been overcome the method is discussed at some length.

Observations were made with a pair of 8 x 50 binoculars, and a 12 volt, 30 watt sealed beam spotlight run off 12 or 17 amp./hr. lead accumulators. Notes were recorded onto a Philips EL01T cassette tape recorder, a note book was used for field sketches, and movements plotted onto a stencil showing the distribution of marked trees.

Habituation of the animal to the presence of the observer is the most common technique used in field studies of behaviour (Schaller 1963, Jolly 1966, van Lawick-Goodall 1968, and Kummer 1968). Some animals are more difficult to habituate than others and Hall (1965) found the patas monkey exceedingly shy while Kaufmann (1962) was never able to habituate solitary male coatis. In the present study habituation of the possum to my presence was slight because of the scattered periods of observation. However, the possum is not an

excessively shy animal and by reducing the disturbing effects of the spotlight and noise I was able to watch even a strange individual without apparently unduly disturbing its normal behaviour.

A number of strategies were used to reduce the disturbing effect of the spotlight. The most effective was to keep the light as dim as possible, and this was done by two methods. A 6.5cm iris diaphragm was hinged to the front of the spot light to give light intensities ranging from full beam when the disphragm was swung aside, effective at 100m, to almost no light for when a possum was within 3m. Secondly a single sheet of orange cellophane over the diaphragm appeared to reduce the disturbing effect of the light. Another strategy was to play the spotlight beam slightly to one side of the possum, so that the animal was on the edge of the pool of light and not in the middle. Finally it was often possible to dispense with the spotlight when the possum was silhouetted against a clear sky, as even with just starlight it was possible to follow the more conspicuous movements of the possum with binoculars.

By using these precautions it was possible to keep the spotlight trained on a possum for two or three hours without apparently disturbing its behaviour. Occasionally, however, when a possum was on the ground it would suddenly appear to become "fed up" with the light and trot rapidly away.

The possums were most sensitive to the spotlight just after they had come out of their dens at dusk. If full beam was used on them then the usual reaction was to return to the den, though this varied greatly from individual to individual. Alice, for example, was particularly shy, not only to the spotlight but to any sound I made. She would return to her den if the spotlight was at all bright while she was anywhere in her den tree, and would sometimes not reappear until 2 hours later. Once when following 15m behind I startled her by dropping my note book. She dashed up a tree to a fork where she sat for six hours gazing at me, her only movement being the occasional turn of her head. Once I had realised just how shy Alice was I could watch her by staying well back (50 to 60m) and by being very careful with the spotlight. At the other extreme was Male 32 who trotted towards me almost immediately the spotlight shone on him, if he was on the ground. He usually came within

5 to 10m and once or twice came right up to sniff at my boots. Most other individuals lay somewhere between these two extremes and it was a matter of adjusting the technique to suit the individual. There appeared to be a tendency for young males to be the least disturbed by my presence as they were the only ones that ever nibbled at my boots, and for the adult females to be most disturbed, with the young females and older males somewhere in between. Alice was the only possum whose behaviour was significantly affected by spotlighting, but by the end of two years I knew her well enough to overcome most of her shyness.

Initially I attempted to keep as close as possible to the possum under observation and was reasonably successful at following several at distances of 10 to 15m when they were travelling on the ground. By being so close, however, there was always the danger that any sudden movement or noise on my part would put the possum to flight, and the probability that my presence significantly reduced social interactions of other possums with the one being followed. Therefore, for the 1966 all-night observations I switched to a policy of keeping well back. On the ground the optimum distance was 40 to 50m which gave a suitable balance between keeping the possum under observation and not disturbing it. This distance could be reduced to 20 to 30m from the base of a tree into which a possum had climbed, to be increased again when the possum showed signs of descending.

Working at these distances many of the finer details of behaviour were lost, but it was considered more important to have an undisturbed population during the 1966 all-night observations. During the more intensive observations of courtship and mother-joey relationships made during 1968 it was sometimes possible to come much closer because of my ability to predict more accurately the movements of the possums, and to position myself accordingly.

During all-night observations one of the biggest difficulties was to maintain a constant standard of observation and recording while following the possum for times ranging from 8 to 11 hours. Luckily a possum spends much of the night resting. During these periods I was able to develop a

Table 2.2

Seasonal distribution of spotlighting observations at Moggill Farm

Dates (Inclusive)				No. of hours Type of observation				
				Watching behaviour	Census	General	Total	Purpose of observations
1965	Jan.	-	Dec.	101	27	43	171	Preliminary
1966	Jan.	-	Dec.	549	27	6	582	All-night general
1967	Jan.	-	Dec.	53	17	8	78	General
1968	Jan.	-	April	57	3	127	187	Courtship and mating
"	May	-	Aug.	-	5	1	6	
1968/9	Sept.	-	Jan.	107	5	24	136	Mother-joey relationships
TOTAL				867	84	209	1160	

technique of relaxing yet at the same time keeping the possum in view. Immediately the possum began to move again I was aware of this and became alert once more. They also have a relatively long rest period in the middle of the night, and once I had recognised this I began to break off observations for half an hour. Occasionally I missed some action because of this but in all cases it appeared to be only a small amount of feeding. Twice during 52 nights of all-night observation I actually fell asleep, each time for half an hour.

When following a particular individual throughout the night recordings were made at approximately 5 minute intervals (determined from a wrist watch) and more frequently if rapid changes in activity or social interactions were occurring.

Comfort and warmth are esstential prerequisites for making good observations over long periods, and these were supplied by a rubber ring air cushion and plenty of warm clothing including a kapok-lined inner-flying suit.

2.22 Chronological Sequence of Observations

Over a period of 4 years a total of 1160 hours was spent in the field observing possums. Observations can be grouped into time spent actually watching the behaviour of possums, time spent on census work, and time on general observations such as transects to determine the distribution of individuals (Table 2.2).

Preliminary observations were made during 1965 to select an area and to develop techniques, particularly those of keeping one possum under observation for long periods of time.

During 1966 a series of all-night observations was made to obtain general patterns of behaviour and social organisation, especially daily and seasonal ones. For 52 weeks, one night a week was spent following an individual from the time it emerged from its den at dusk until it returned just before dawn. A group of six neighbouring individuals, 3 males (Jack, Gus and Alec) and 3 females (Jill, Gert and Alice) were used for these all-night observations. Each week a different individual was followed,

with the sexes alternating. Thus it took six weeks to complete one round of the six individuals, maintaining the same sequence of individuals watched from round to round, except for the occasional change owing to unforseen circumstances. Although this meant that the same individual was followed only once every six weeks, at least one of the others was usually within observational distance for part of the night, and sometimes throughout the night.

During the 1967 observations the same six individuals were followed from week to week, but the time of observations was shortened to 2 to 3 hours from dusk. These observations were to continue the study of the social structure of the population over a longer period than one year.

Between January 29 and April 19th 1968, a series of observations were made to examine the interactions between males and females just before and during the main breeding season. The observations were divided into two sections, one to follow the activities of males in relation to a selected female, and the other to check the activity of all the possums in the study area. On two nights a week one of four adult females was watched for two to three hours from the time she left her den at dusk, and the reactions of males to her and to each other in her vicinity were recorded. On two other nights of the week the whole study population was checked for courting activity by making 2 rounds of the area per night. Each round lasted from 2 to 2½ hours, the first starting at 19.30 which is about 1½ hours after the possums had emerged from their dens and allowed a male time to pair-up with a female. The second round started at 23.00. The route followed for the two rounds was the same on any one night, but reversed on alternate nights. When a male and female were found in the same tree their activity was checked by switching the spotlight off for 10 minutes. This being the time considered sufficient for the possums to resume any behaviour interrupted by my approach.

Mother-joey relationships were subject to intensive observations from September 1968 to January 1969. Late August early September is when the main crop of joeys begin to leave their mother's pouch. Two or three times a

Figure 2.7: Brush-tail possum in a wire mesh cage trap used during the study.

week one of four females was kept under constant observation for 90 minutes from the time it came out of its den, and a running commentary of her and her joey's behaviour dictated into a tape recorder. Occasional early morning observations were also made. No attempt was made to study mother-joey relationships up to the time that joeys began to come out of the pouch, and any observations for this period of development were incidental to other observations.

2.23 Capture

Capture of possums was kept to a minimum to avoid undue disturbance to the population. Its purpose was the capture of individuals for marking, ageing, and in the case of females to check for the presence of young in the pouch. Trapping was not carried out at the same time as behavioural observations and at least one night was allowed to lapse between trapping and observations.

Wire mesh traps (60 x 20 x 20cm) baited with apple or bread and jam were used (Fig. 2.7). They were not set in any geometrical pattern, but where it was judged they would be most likely to capture the individuals desired. A captured individual was transfered to a sack in which it usually remained sufficiently quiet for superficial examination and even for the measuring of pouch young. However, prior to marking and ageing the animal was anaesthetised with ether. To do this a 500ml jam jar containing a wad of cotton wool and ether was slipped over the possum's nose.

Throughout, emphasis was placed on handling the possum as gently as possible to minimise unpleasant associations between the observer and his subjects, and the restraining methods used by Dunnet (1956) and Taylor and Magnussen (1965) were avoided. For instance when transferred from the trap to the sack the possum was not pulled or shaken out of the trap, but instead the bag lowered over the animal in the trap and gently worked underneath it. Also the jar of ether was allowed to rest gently on the animal's nose and not forced tightly over it. Occasionally an individual, especially adult males, would struggle violently just before becoming anaesthetised completely and the animal had to be held firmly. To overcome this struggling, adult

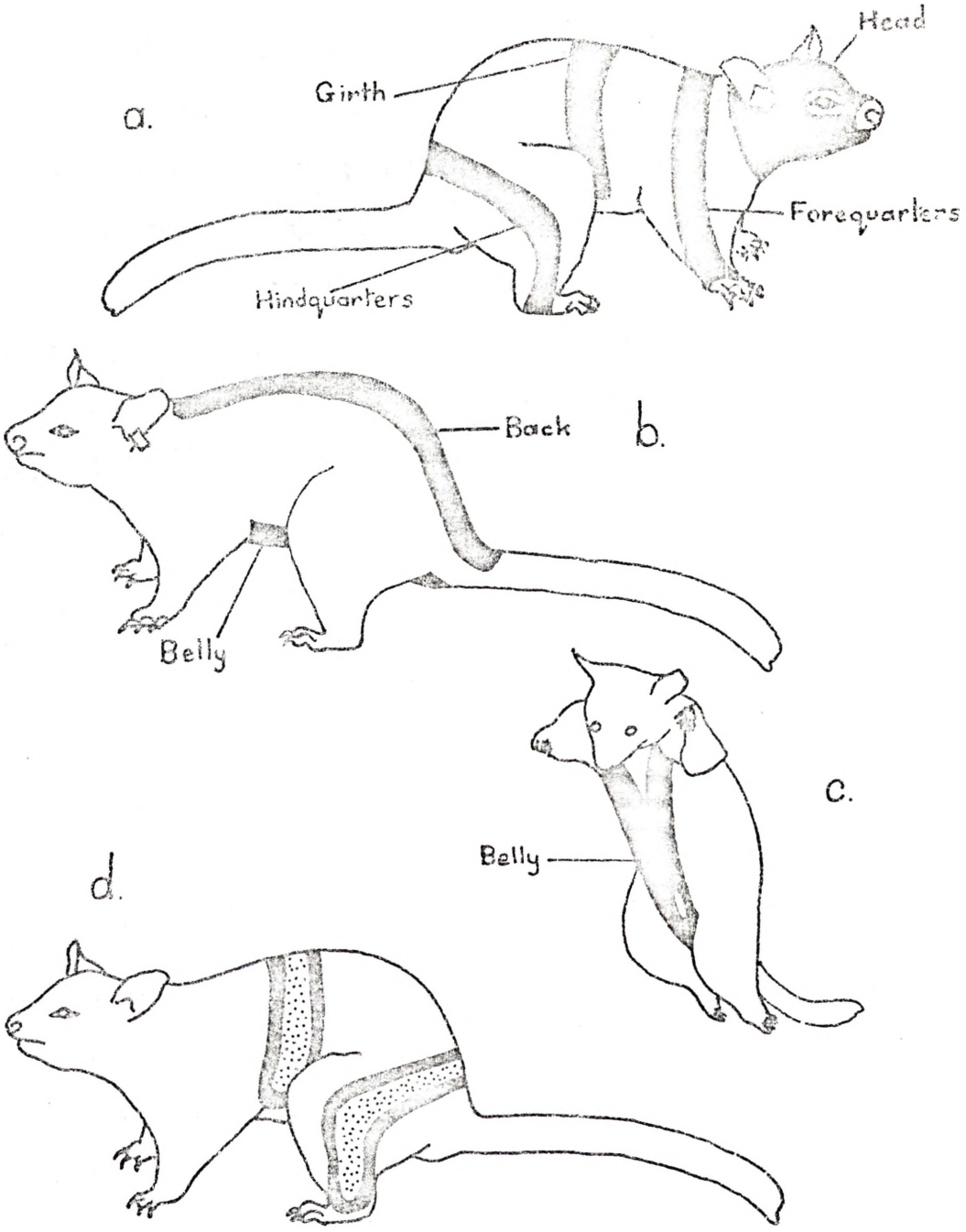


Figure 2.8: Fur dye patterns used to individually mark Trichosurus vulpecula. Fresh dye shaded; new undyed fur stippled.

males were usually initially anaesthetised with ethyl chloride which caused little struggling, but did cause the animal to stiffen. Once anaesthetised they were then switched to ether and the muscles relaxed.

It was possible to mesmerise possums by keeping the full beam of the spotlight shining directly in their eyes. If they were on low branches or fence railings they could be approached and caught by the tail. It was even possible to do this with Juveniles (6-10 months old) on the ground but never adults. However, this method of capturing possums was quickly discontinued because of the probably unpleasant association with the spotlight.

2.24 Marking

Individual recognition was the key to the whole study and possums were marked in several ways, each of which had its advantages and limitations.

2.241 Fur Dyeing

Fur dyeing was used to recognise individuals at distances of up to 100m. It had, however, a limited life. Durafur Black R manufactured by Imperial Chemical Industries was used to dye the fur of a possum and applied according to the directions given by Rowley (1956) with some modifications. Trial and error indicated that the best results were obtained when the dye and hydrogen peroxide were made up with warm water and applied no sooner than 1½ hours and no later than 6 hours after being made up. Detergent was not added to the dye as suggested by Rowley. Instead the fur to be dyed was first thoroughly wetted with a dilute solution of detergent and then rubbed almost dry. Excess dye was daubed over the wet fur, taking care none ran into the dry fur, and allowed to soak in for about half a minute before being dabbed dry.

Six dye patterns were used, either alone or in combination (Fig. 2.8).

Dots and thin double lines were of no use because moulting rapidly made most dye patterns patchy. The six patterns shown could still be recognised with up to 75% of the dye obliterated thus giving the patterns an effective life of five months (Table 2.3). Moulting was the main cause of pattern obliteration and in some cases closely followed the dye pattern

itself (Fig. 2.8d) strongly suggesting that the dye had caused the moult. Despite this effect of the dye on moulting the possum did not appear to be irritated by the dye.

Table 2.3

Number of individuals in which it was possible to correctly identify the dye pattern at monthly intervals following the application of the dye. Dotted line represents the effective life expectancy of the dye.

Time after dyeing (Months)	No. of individuals in which dye pattern was:- Adequate	Inadequate
1	5	0
2	12	0
3	12	0
4	16	1
5	20	3
6	6	5
7	6	2
8	5	3
9	-	-
10	3	3
11	1	3
12-19	0	12

2.242 Ear Tagging

Numbered monel metal fingerling tags (15 x 3mm) supplied by Salt Lake Stamp Co., Utah, were clipped to the proximal half of the ear. Each tag had two different colours of scotchlight reflecting tape glued to the plain side of the tag, and attached to the ear with the reflecting tape facing forward. Eighty combinations were obtained by using five colours (red, green, blue, yellow, and white), four ear positions (top left, top right, bottom left, and bottom right), and with different orientations of the two colours on the tag (e.g. white on red, red on white). Although some ear tags remained in for the duration of the study others were either lost or pulled out in a matter of months.

Tags allowed individual recognition at distances of up to 30m but only from in front. They were invaluable when a possum in a tree needed to be identified quickly, as in censuses. The characteristic position of

a possum in a tree looking down at the observer nearly always exposed the ears, and hence the tags, whereas the dye pattern of a crouched animal in a tree was not always possible to determine.

2.243 Ear Clipping and Tattooing

In an attempt to obtain a permanent individual marking system first ear clipping then tattooing were used.

Notches were clipped in the ear using 4 different positions on each ear. The notches had to be an oblong about 3mm. wide and 4mm. deep taken from the margin of the ear as a V shaped notch soon became hard to differentiate from a natural tear, and a semicircular notch tended to grow out and the outline merge with that of the ear thus making the notch hard to distinguish. To prevent bleeding the notches were cut with heated end-cutting pliers.

Numbers about 15mm high were tattooed on the inner surface of the ear, tens on the left and units on the right ear. To do this the number was traced out in indian ink on the ear which was then pierced many times along the ink line with a mounted needle to form a tattooed line 2-3 punctures wide.

Although tattooing was started in December 1966 ear clipping was not discontinued until towards the end of the study, because there was some doubt that the tattooed numbers would still be clear after a year or more. There was a tendency for the numbers to thicken and to become blurred, but the numbers were large enough for this to be irrelevant so that even after three years they could still be read (Table 2.4). The only exceptions were one adult which lost that part of the ear with the number and two individuals that had been tattooed at 5-6 months. In these two young possums the black dots of the tattoo became more and more dispersed as the ear grew until the numbers became obscure.

Tattooing, therefore, is a satisfactory permanent marking system for adult possums and preferable to ear clipping because it does not mutilate the animal. The numbers should be as large as possible to offset the effect of blurring with age, and it should not be used on ears which are still growing.

Both earclipping and tattooing were done on anaesthetised animals.

Table 2.4

Permanency of ear tattooing as indicated by the proportion of correct readings (determined by ear notches) made at the last examination of a tattoo.

Time between tattooing and last reading (months)	Number of correct readings	Number of incorrect or doubtful readings
1 - 6	7	2+
7 - 12	7	-
13 - 18	9	1:
19 - 24	7	-
25 - 30	3	-
31 - 36	4	-
Total	35	3

+ Possum tattooed when 5-6 months old.
: Part of ear with tattoo lost.

2.25 Ageing

Pouch young were aged to the nearest day on head length using the nomogram of Lyne and Verhagen (1957).

Table 2.5

The error for ageing pouch young from Moggill Farm by head length on the nomogram of Lyne and Verhagen (1957), expressed as the difference between the known interval and estimated interval of the first and last ageing of a pouch young.

Estimated ages	Interval (days) Estimated	Known	Difference (days)
1 and 113	112	114	2
2 " 94	92	88	4
7 " 91	84	76	8
8 " 119	111	120	9
9 " 151	142	154	12
11 " 136	125	134	9
16 " 82	66	63	3
28 " 96	68	70	2
36 " 68	32	28	4
47 " 160	113	121	8
54 " 79	25	24	1
68 " 75	7	6	1
71 " 157	86	88	2
73 " 97	24	24	0
96 " 126	30	42	12
110 " 130	20	23	3

Difference: Mean 5.0±0.97, S.D. 3.889

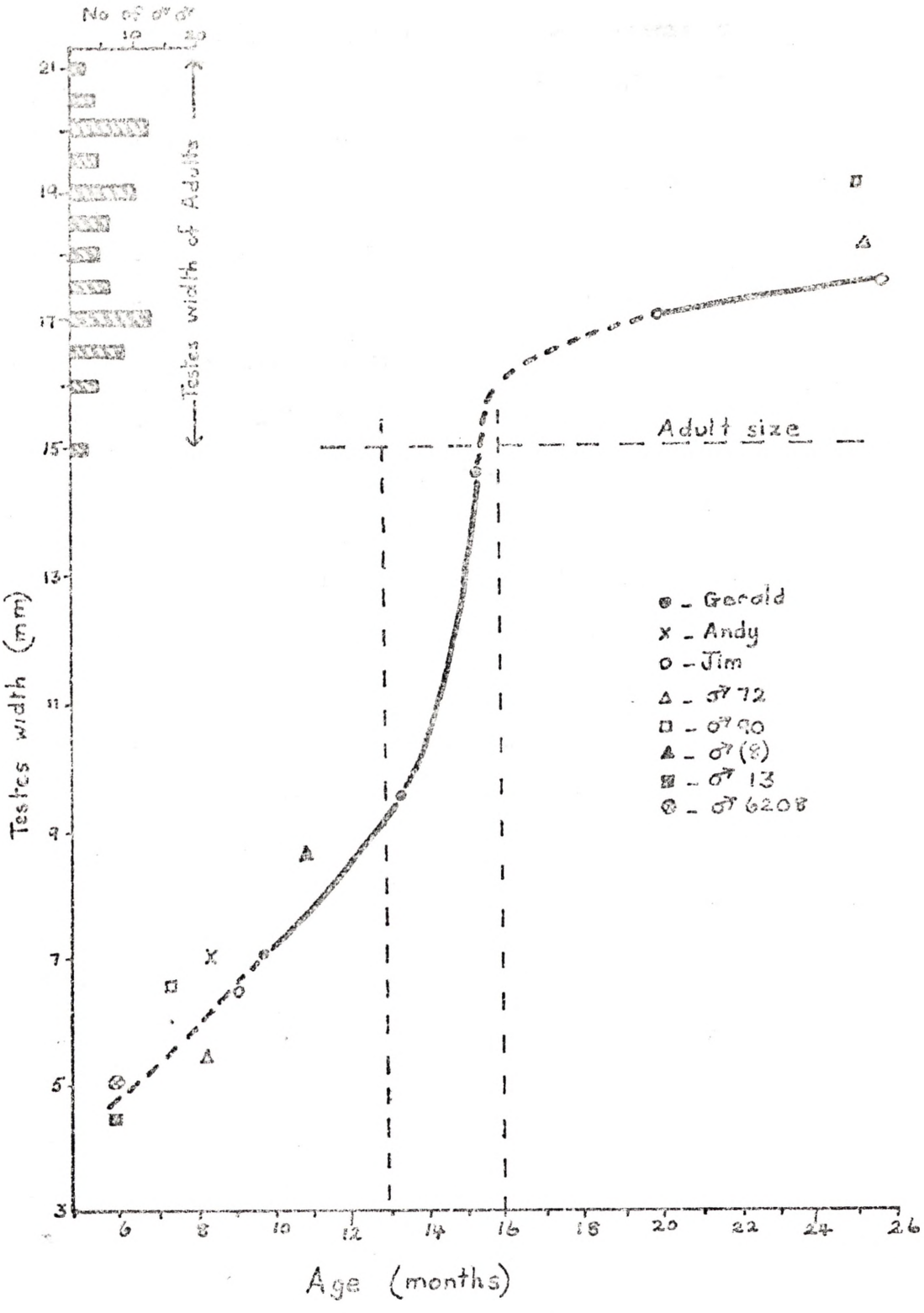


Figure 2.9: Testes width measured through the scrotum to show the relationship between testes size and age. Note the rapid increase in size between 13 and 16 months to reach adult size. Line fitted by eye.

Insufficient measurements were made on any one individual to compare the growth of pouch young in the study population with those measured by the above authors. But by comparing known time intervals obtained from the nomogram a mean difference of 5.0 days was obtained (Table 2.5). Thus ages of pouch young have a mean error factor of ± 2.5 days.

Adults were aged on tooth wear using a modified version of the method used by Thomson and Owen (1964) (see Appendix I), and juveniles on a combination of tooth wear, tooth erruption (Kingsmill 1962), and in males the rapid increase in the growth of the testes (Fig. 2.9).

2.26 Reproductive condition of Females

Any reference to the oestrous cycle in females is not based on physiological measurements, but is inferred from the estimated date of birth of joeys, the length of the gestation period (17.5 days) (Lyne, Pilton & Sharman 1959, Pilton and Sharman 1962), and the length of the oestrous cycle (25.69 ± 0.31 days) (Pilton and Sharman 1962).

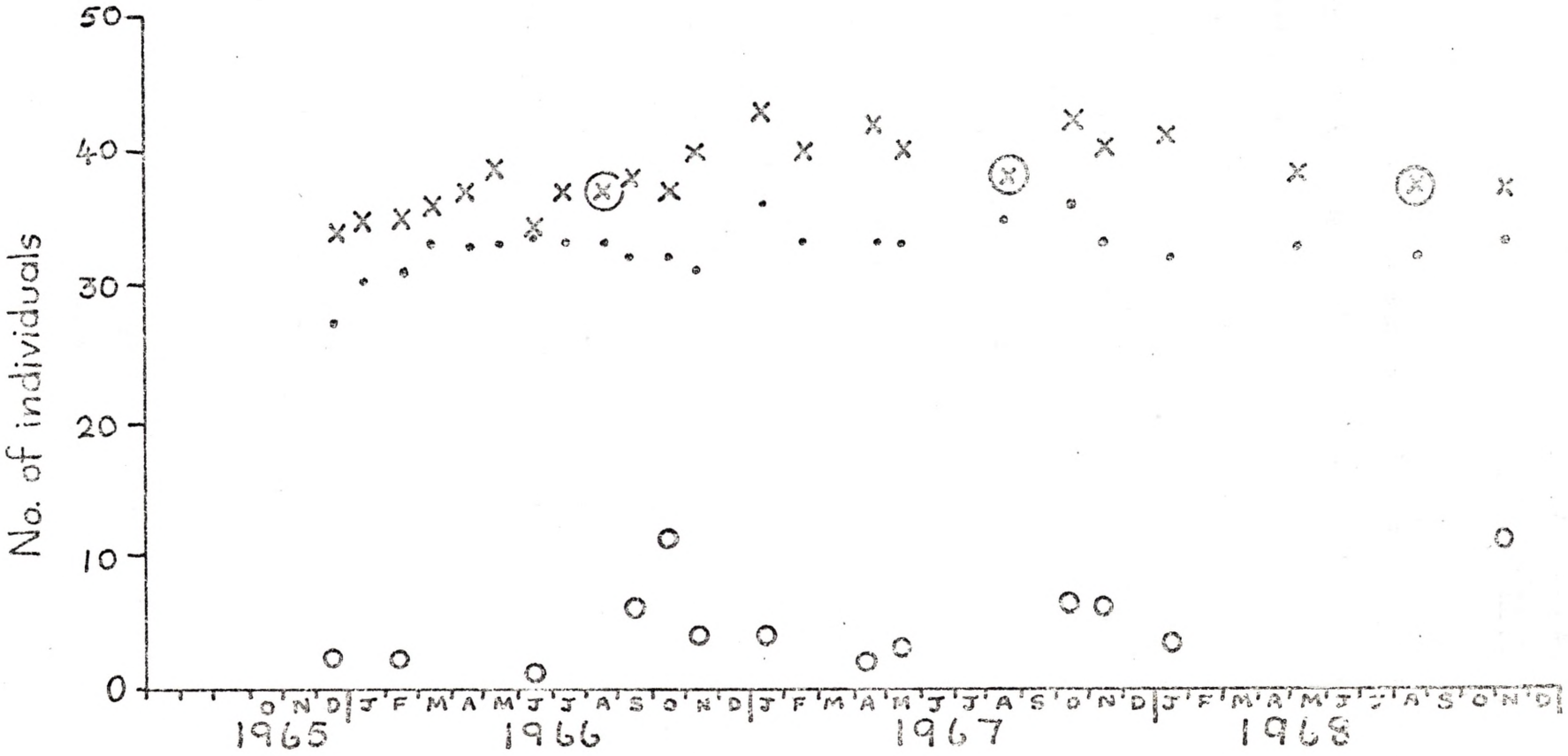


Figure 3.1 : Number of possums known to be in the 17.3 ha study area at the time of the census transects. Dot = marked adults plus independent juveniles; cross = total adults plus juveniles; circled cross = August census; open circle = dependent juveniles.

CHAPTER 3

THE POPULATION STUDIED

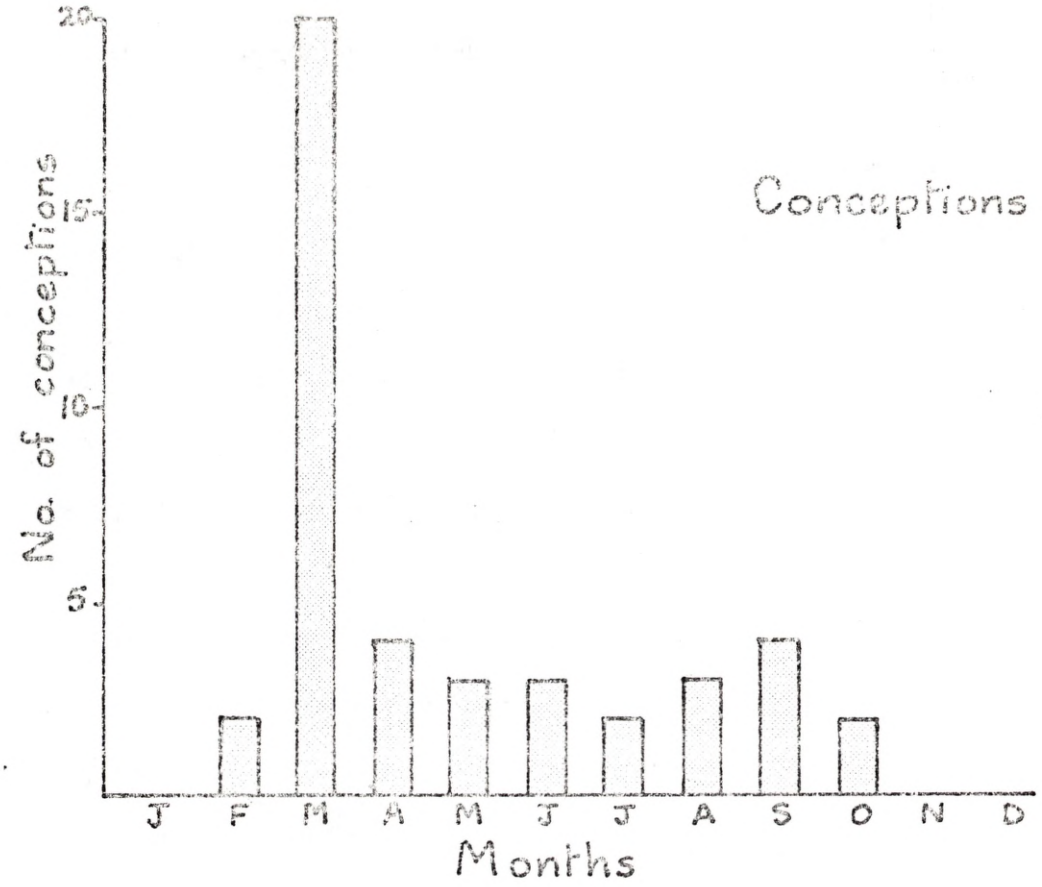
3.1 POPULATION DENSITY

To census the population, spotlight transects of the area were made, following the same route each time. Spot-lighting began about 1½ hours after dark. This was to allow possums to move away from their den trees, as some possums, especially females, re-entered their dens if they were still in their den trees when approached.

Transects lasted about 2 hours from beginning to end and were started in June 1965. For the first nine weeks they were repeated weekly, thereafter they were repeated at approximately monthly intervals until the end of 1967, and at less frequent intervals during 1968.

The number of individuals in the area at the time of the transect was taken to be the number of marked individuals known to be alive, plus the number of unmarked individuals seen during the transect. Two age categories were recognised. (1) adults plus independent juveniles; (2) dependent juveniles — defined as young either riding on the back of a female, in the same tree as a female, or within 10m of a female on the ground. A possum was considered to be still in the area for two months after it was last observed within the area, either during a transect or at any other time.

It is apparent (Fig. 3.1) that over the period of the study, the population remained stable. This is particularly noticeable if the three August censuses are considered in which population estimates of 37, 38, 37 were obtained for 1966, 1967 and 1968 respectively. August is considered to be an appropriate month in which to make comparative population estimates, because by the end of August the main crop of joeys born in March-April are beginning to emerge from the pouch. Thus from September onwards new individuals are being added to the counted population which accounts for the generally higher estimates at other times of the year, but by the following August the population has declined to apparently the lowest level prior to a new batch of individuals being added. The fluctuations



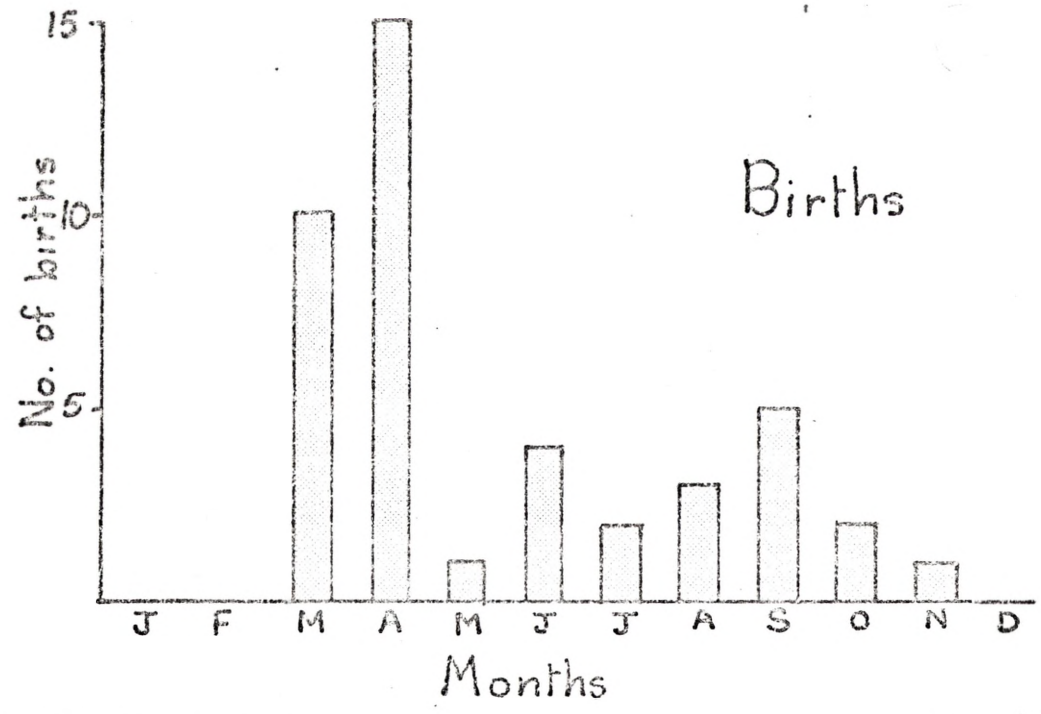


Figure 3.2 : Seasonal distribution of births and conceptions, expressed as combined monthly totals for 1965, 1966, and 1967. Conception taken as being 17 days prior to estimated date of birth.

appear to be of a minor nature and do not represent any major yearly fluctuations of the population.

Although dependent juveniles are present in many months of the year, there does appear to be a greater number during September, October and November (Fig. 3.1).

The densities of 2.14, 2.19, and 2.14 possums per hectare for the Augusts of 1966, 1967, and 1968 at Moggill Farm are roughly equivalent to the densities found by Dunnett (1964) in his Canberra studies. He trapped 16 possums in 8.5 acres of his area VIII during 18 months giving a density of 1.88/acre (4.65/ha), which was the maximum in his study area. The overall population density was 0.43/ha (extracted from Dunnett 1964).

On the other hand Moggill Farm possum densities are much lower than those recorded in New Zealand where densities of 30/ha (Batcheler et. al. 1964) have been recorded. Even in areas where possums have been established for 70-80 years, and are presumably relatively stable, densities of 10.6/ha are known (Crawley 1973).

3.2 BREEDING

Births occurred in all months except the three summer months of December, January and February (Fig. 3.2). A very definite autumn peak followed the summer period then dropped to a low level with the suggestion of a second modal peak in September.

A pronounced autumn peak of births following an almost total lack of births during the summer is characteristic of populations so far studied both in Australia (Dunnet 1956, 1964 and Smith et. al. 1969) and New Zealand (Tyndale-Biscoe 1956, and Crawley 1973), except in the Adelaide region of Australia where the Autumn peak was far less pronounced (Pilton and Sharman 1962). A second less pronounced breeding season in spring has been recorded at Canberra (Dunnet 1956, 1964) parts of New South Wales (Smith et. al. 1969) and in New Zealand (Gilmore 1969), but it does not occur in all populations especially when densities are high (Crawley 1973).

The spring peak is mainly the result of females breeding for a second time in the year after the joey born in autumn has left the pouch. The

frequency of double breeding at Moggill Farm was 25 observations of one joey and 7 observations of two joeys born in the one year, a 22% incidence of double breeding. Kean (1971) has obtained a rate of double breeding as low as 1 in 8000 in a New Zealand population, nor did Crawley (1973) record any double breeders in the Crongorongo population. Double breeders appear to be a feature of relatively low density populations (Kean 1971).

No multiple births were recorded out of the 88 pouch young observed. Twins appear to be rare irrespective of the density of the population. Kean (1971) for example recorded only one set of twins in the 8000 records of breeding obtained from the Crongorongo population.

Sex ratio of the 43 pouch young used to construct the histograms, and of adults plus independent juveniles (as defined in the population estimates) for August 1966, 1967 and 1968 at no time differed significantly from parity (Table 3.1).

Table 3.1

Sex ratio of pouch young and of adult plus independent juveniles.

		Males	Females	p.
Pouch young		17	23	>.1
Adults	1966	16	21	>.5
	1967	19	18	>.9
	1968	13	23	>.1

In studies with large samples the sex ratio of pouch young has consistently favoured males (Caughley and Kean 1964; Hope 1972) and for pouch young 0-50 days old this disparity was found to be significant (Hope 1973). However, differential pouch mortality resulted in parity of the sex ratio by late pouch life, except from one locality on Kangaroo Island where the excess of males (202 males, 92 females) was highly significant (Hope 1973). It is apparent therefore that the Moggill Farm population follows the general trend of a 1:1 adult sex ratio.

Breeding at Moggill Farm has also been expressed as the distribution of conceptions as this was often a more valid comparison with the seasonal distribution of certain behaviours. The histogram (Fig. 3.2) has been constructed from exactly the same data as the births histogram with an

appropriate allowance of 17 days for the gestation period. The different configuration for the two histograms is an artifact of clumping the data into months. The shift to the left of one month is the significant difference between the two.

3.3 SEXUAL DIMORPHISM

A slight but significant sexual dimorphism in size exists with the male having a mean weight of 2.51kg (S.E. 0.08) and the female 2.12kg (S.E. 0.05) (Table 3.2). A measurement less suoject to fluctuation is the head width with males having significantly wider heads (mean 54.17 mm S.E. 0.48) than the females (mean 51.50 mm S.E. 0.34) (Table 3.3).

Table 3.2

Weights of T. vulpecula at Moggill Farm, estimated to be 2 years of age and older. Females with joeys in the pouch not included.

Weight (Kg)	
Males	Females
2.55	2.10
1.95	2.15
2.95	2.45
3.10	2.60
2.10	2.15
2.45	1.85
2.90	1.90
1.75	2.40
2.90	2.25
2.80	1.75
2.35	2.10
2.70	2.10
2.60	2.05
2.70	2.30
2.60	1.80
2.10	2.00
2.20	1.90
2.30	2.35
2.25	
2.80	
2.60	
no. 21	18
mean 2.51	2.12
St.d. 0.35	0.23
S.E. 0.08	0.05
Range 1.75 to 3.10	1.75 to 2.60

Males:Females F=15.0693, d.f. 1,37, p <.001 +++
(Single classification anova Sokal and Rohlf 1969)

Note: + is used instead of the conventional asterisk to denote the level of probability in tables.

Table 3.3

Head width across the zygomatic arch of T.vulpecula at Morgiil Farm, estimated to be 2 years and older.

Head width (mm)	
Males	Females
55.0	52.5
51.5	52.0
57.5	53.5
56.5	52.5
51.5	53.5
53.0	53.0
56.0	53.0
50.0	49.0
57.5	50.5
55.0	52.0
53.5	53.5
57.5	49.0
52.5	51.5
55.0	50.5
53.0	50.5
51.0	51.0
55.0	50.0
52.5	49.5
53.0	53.0
55.0	50.0
56.0	50.0
	56.0
	52.5
	51.0
	54.0
	50.5
	49.5
	48.5
No. 21	28
mean 54.17	51.50
St.d. 2.19	1.79
S.E. 0.48	0.34
range 50.0 to 57.5	48.5 to 56.0

Males:Females F=21.0903, d.f. 1,47, $p < .001$ +++

(Single classification anova Sokal and Rohlf 1969)

The general colouring of the upper parts of a brush-tail possum is a light grey, with a black tail and a pale silvery white to cream coloured belly with a chestnut coloured patch of fur running longitudinally mid-vertrally on the thorax, which is the sternal gland. In the males the sternal gland is larger and greasier then in females (Bolliger and Hardy 1944). There is also a tendency for older males to take on a rufous tinge to the dorsal fur particularly over the shoulders.

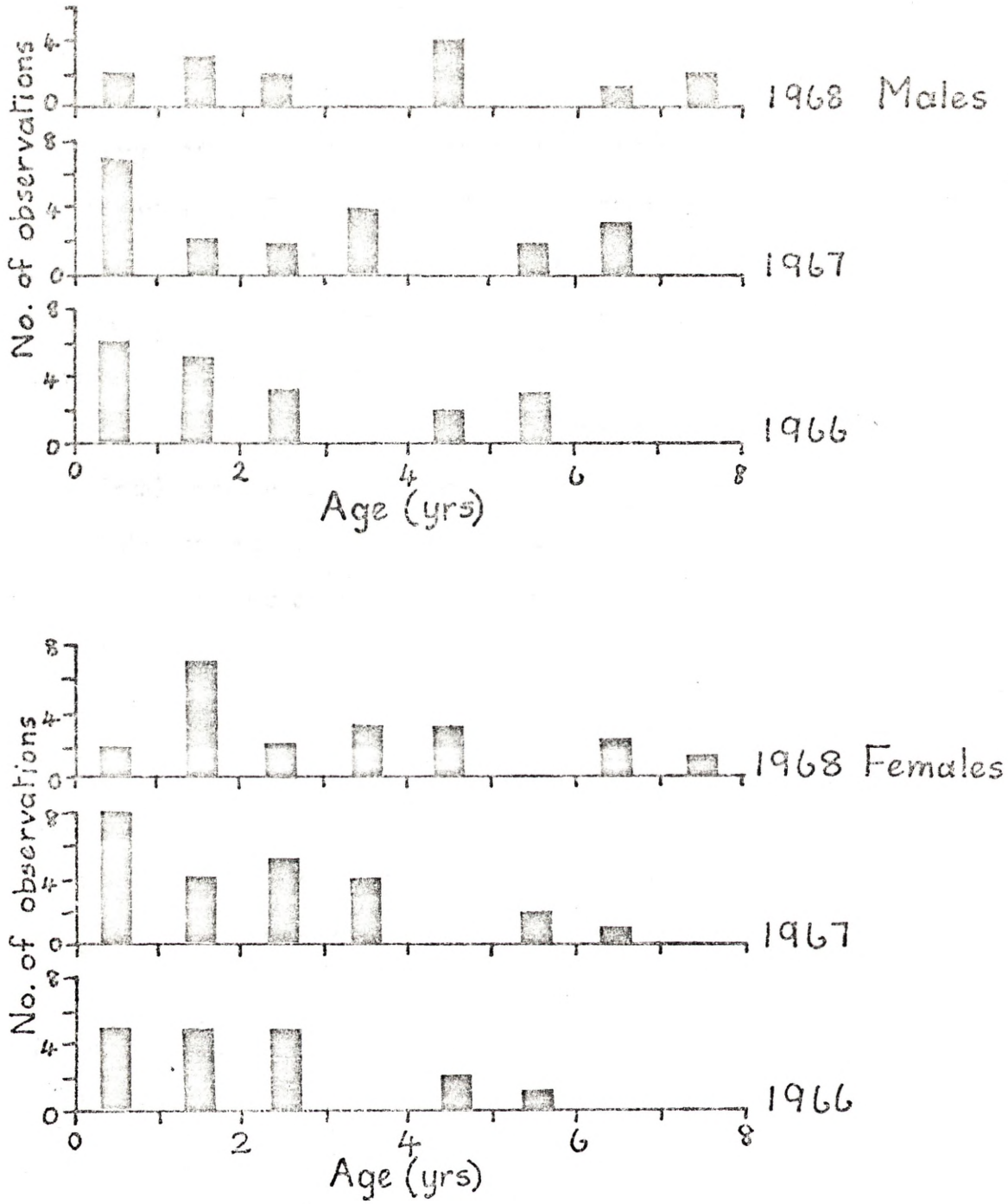


Figure 3.3 : Age structure of the population for February of three consecutive years.

3.4 AGE STRUCTURE

The age structure of the population at Moggill Farm is given in Figure 3.3 for the three years 1966, 1967 and 1968. It is shown for February of each year which is immediately before the main breeding season. With the low sample sizes the only conclusion that can be drawn is that most of the population is in the first five year classes, and a few reach the 8th year class.

Individuals 6 years old have been recorded at Canberra (MacLean 1967), and in New Zealand a 12 yr old individual has been recorded (Crawley 1970). These known age spans indicate that the estimated ages of up to 7 years at Moggill Farm are within the known life span of the brush-tail possum in the wild.

3.5 POPULATION LOSSES

Data were too few to allow a statistical assessment of population losses, especially as there is a sex differential dispersal of young possums (Ch. 6.5) and the study concentrated on behaviour and not on the collection of population data.

The cause of a possum disappearing was assumed to be predominantly mortality, except in the case of juvenile males, who disperse from their maternal area (Ch. 6.5). There were also a few cases of adults shifting home ranges (Ch. 6.42 and 6.51) but this probably is not a significant factor in a relatively stable population.

The actual cause of mortality was not known except in one possible case of poisoning, and three deaths induced by the study methods. On the 28th March 1968 Male 6228 was observed at the foot of a tree lying on his belly. When he got up and began to trot, his back legs appeared to be partly paralysed. Although he was slow and clumsy and seemed to have little control of his hind legs he managed to climb a vertical tree trunk to a branch 1-2m off the ground. At the foot of the tree where I first saw Male 6228 was a creeper of Passiflora suberosa, bearing juicy black berries. It is possible that the male had been eating the berries which contain HCN cyanogenetic glycosides (Everist, 1974). A staggering gait

Table 3.4

1966 observations of the time that adult possums emerged from their dens at dusk, in relation to astronomical twilight. Astronomical twilight readings for Brisbane supplied by Astronomer's Association, Queensland. Differences between sexes tested for with one way analysis of variance (Sokal and Rohlf 1969)

Time of observations + (min)							
Male				Female			
70	47	56	63	67	57	45	48
5	47	48	59	39	54	35	49
54	45	47		52	44	48	36
47	57	50		57	49	47	50
49	36	45		57	45	53	64
47	47	42		28	36	46	60
48	36	51		44	35	31	61
48	48	34		46	32	18	60
42	36	57		50	56	55	50
48	48	56		43	1	35	
47	41	54		45	31	48	
34	35	48		42	38	66	
46	41	60		42	1	54	
43	40	61		35	52	60	
37	36	48		52	37	61	
33	45	51		44	43	58	
35	42	51		44	46	60	
30	48	47		45	46	69	
50	49	56		43	50	68	
11	45	61		44	48	57	
No.	62			69			
Mean	45.8			46.6			
S.D.	10.629			12.825			
S.E.	1.3			1.5			
Range	70 to 5			69 to 1			
Variance	112.981			164.482			

$F = 0.138$, d.f. = 1,129, $p > .50$ n.s.

\+ all observations before astronomical twilight.

Table 3.5

1966 observations of the time that adult possums returned to their dens at dawn in relation to astronomical twilight. + = min before twilight, - = min after twilight. Differences between sexes tested for with one way analysis of variance (Sokal and Rohlf 1969)

Time of observations (min)						
Male			Female			
-45	+49	-46	-51	-20	+23	-16
-18	+38	-58	+14	+42	+24	-11
+ 4	+10	-57	+14	+32	+11	-11
-15	-14	-27	- 4	+12	+30	- 6
+ 5	+34	0	-14	+ 6	+29	-20
-25	+33	-26	+ 3	+33	+41	-24
+ 7	+71	-48	+ 8	+29	+73	-40
-19	+ 4	-48	+89	+18	0	-26
-32	-13	-63	+74	- 8	+23	-55
- 4	- 3	- 3	+35	+192	+62	-23
-25	-12		+168	+10	+48	-51
+ 5	-46		-16	+105	+35	-18
+11	+11		- 3	+70	-26	-32
+76	-10		+23	+39	+239	+ 7
+98	-26		+ 7	+80	+ 1	+11
-14	-45		+26	+52	+109	-30
+10	-28		+ 5	+41	- 2	+ 8
+46	-15		+36	+45	-49	+65
+ 8	-33		+13	+30	-24	+ 2
+81	-47		+88	+47	+ 3	-36
						-43
						-27
No.	50		82			
Mean	-5.28		+20.02			
S.D.	36.96		50.65			
S.E.	5.23		5.59			
Range	+98 to - 63		+239 to -55			
Variance	1366.282		2564.900			

$F = 9.279$, 1,130 d.f., $p < .005$ +++

is one of the symptoms of poisoning due to HCN (Gardner and Dennetts 1956). However, paralysis of the hind limbs is also caused by the tick Ixodes sp. Male 6228 was presumed to have died as he was not seen again.

Another two deaths were caused by bee stings. Both possums attempted to enter cavities containing the introduced honey bee (Apis mellifica) when they were released from a trap during the day. One was found dead at the foot of the tree a few hours later, and the other disappeared, presumed dead.

Finally one possum (Gus) was accidently given an overdose of ether when being dyed.

3.6 ACTIVITY

3.61 Leaving and entering dens

The brush-tail possum is strictly a nocturnal animal. Males and females emerge from their dens a mean 45.77±1.35 min and 46.55±1.54 min respectively before astronomical twilight with no significant difference in the time of emergence between the sexes (Table 3.4). This is just as the last traces of daylight in the western sky disappear and it is just past the time when an observer would be able to see a possum without the aid of a spotlight.

Weather was not observed to have any marked effect on the time of emergence, except for heavy continuous rain. On one night heavy rain, which had started during the afternoon, continued unabated until 39-40 min after the mean emergence time of the possums, then eased to a drizzle which finally stopped 20 min later. No possums were seen out of their dens during the heavy rain. The first to emerge did so just as the heavy rain eased to a drizzle. However, this possum was unusually early for the night (possibly owing to an agonistic interaction) because others did not emerge until 22, 38, 40, 42 and 64 min after astronomical twilight. Heavy rain which came late in the night did not drive the possums back to their dens. Instead they crouched on a branch with head hanging in the resting position (see Appendix II).

Possums began to return to their dens well before dawn, but with

considerable variation in the time. Females returned a mean of 20.02±5.59 min before astronomical twilight, and ranging from as early as 239 min before to 59 min after twilight (Table 3.5). The mean times of return was well before I could detect any lightening of the eastern sky. Males returned to their dens significantly later than females with a mean time of 5.28±5.23 min after twilight and with a range of 93 min before to 63 min after twilight (Table 3.5).

The low standard deviation about the mean time in relation to astronomical twilight, of emergence at dusk (Table 3.4) suggests that emergence is triggered by a change in light intensity. The return to the dens in the early morning, however, does not have an obvious relationship with light apart from the fact that when dawn does begin to break, any possums still out hurry back to their dens. The relationship is not apparent, especially with the females, because not only have most possums returned to their dens well before any lightening of the sky is observed, but also because the variance in the time of return at dawn is significantly greater compared with the time of emergence (Table 3.6).

Table 3.6

The variance ratio as an indication of the difference between variances of times of emergence from a den and return to a den. (Data from Tables 3.4 and 3.5).

Variances tested			Variance ratio	Degrees of Freedom	P (Two tailed test)
Female emergence Male emergence	164.482 112.981	=	1.4558	68 61	>.25 <.1
Female return Male return	2564.900 1366.282	=	1.8773	81 49	>.025 <.05+
Male return Male emergence	1366.282 112.981	=	12.093	49 61	<.001+++
Female return Female emergence	2564.900 164.482	=	15.594	81 68	<.001+++

The greater variation in the time of return can be partly if not wholly explained by a number of factors. First, at dusk all possums are in their dens whereas in the morning, the possums will be at variable

distances from them. Secondly, in the morning there is likely to be a greater probability of delays caused by a number of extrinsic factors such as the presence of predators, my own presence which obviously delayed a possum's return on a number of occasions, and interactions with other possums, particularly at dens. Thirdly, intrinsic factors such as the degree of hunger and individual idiosyncrasies are likely to result in less variation in the time of emergence than the time of return, because the time spent in the den during the day will be less variable to the possum than the night's activity. These factors may explain the greater variation in the time of return, but they do not satisfactorily explain the return of females to their dens well before it begins to get light. The later return of males to their dens is considered to be caused by social interactions between males and females as discussed in Chapter 6.3.

Occasionally possums were seen out of dens during the day. However, wherever the context was known the possum's emergence was always the result of agonistic interactions between two possums sharing a den. The female who lived in the ceiling of the house at Tyne St. several times drove the male out during the afternoon when he was sharing the ceiling with her. He immediately moved to an alternative den. She similarly was known to occasionally evict her juveniles during the day when the mother-joey bond was breaking down.

3.62 Activity during the night

During the all-night observations of 1966 a possum's behaviour was recorded every 5-6 min or more frequently if changes of activity were taking place. The general activities recorded are as follows.

(1) Sitting - this included resting and dozing (Ch. II.1). If a possum was feeding or grooming while sitting the more active behaviour was recorded.

(2) Grooming - this was all self grooming. Allogrooming was confined to mother-young pairs and was not recorded in this series of observations.

(3) Feeding - separated into feeding in a tree which was relatively easy to determine, and feeding on the ground which was easily confused

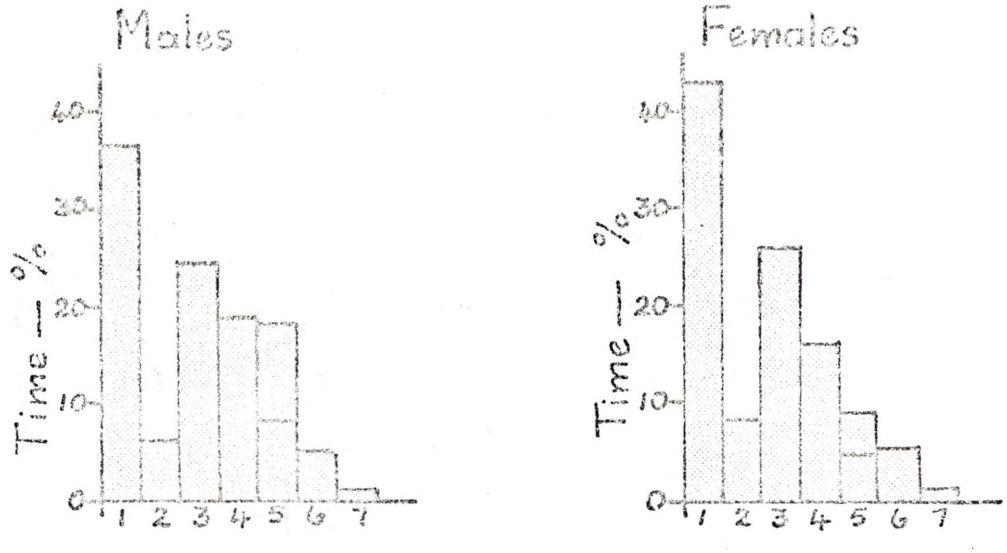


Figure 3.4 : Activity of possums during the night expressed as a percentage of tenth hour periods in which the activity was recorded. 1 = sitting, 2 = grooming, 3 = tree feeding, 4 = travelling in tree, 5 = travelling on ground (lower part = ground feeding), 6 = miscellaneous and ?, 7 = social interactions.

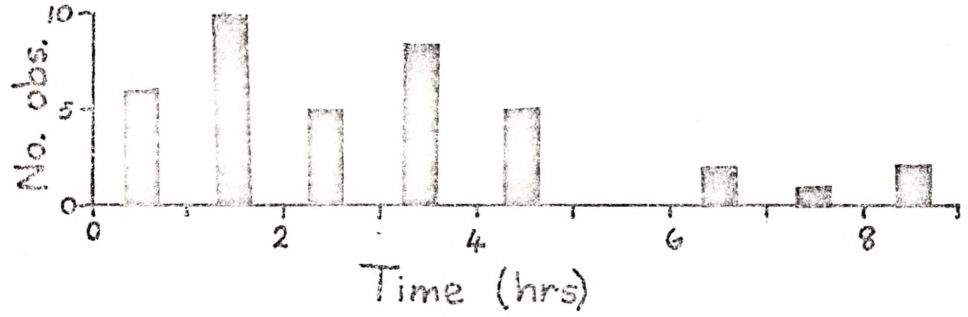


Figure 3.5 : Time that furthest distance from den tree is reached.

with substrate sniffing.

(4) Travelling - separated into tree and ground travelling.

(5) Miscellaneous and unknown - included time spent in a den and short periods of time (<0.5 hr) when the activity was not known.

In all the above the activity recorded as taking place was the main one at the time. For example a possum sitting briefly (<0.25 min) between feeding bouts was not recorded as sitting, nor was a travelling possum which paused briefly to scratch recorded as grooming.

(6) Social interactions - only definable interactions such as mounting and agonistic interactions (Ch. 5.16) were recorded.

For the purpose of analysis an hour was divided into tenths. Activity was then recorded as having taken place during a particular tenth. Nights when a possum appeared excessively disturbed by the presence of the observer, or was mislaid for more than an hour, were eliminated from the sample. This left a total of 36 nights: 7 nights with Gus, 5 with Alec, 5 with Jack, 7 with Gert, 6 with Jill and 6 with Alice.

Figure 3.4 gives the percentage of tenth hour periods in which the above activities were recorded, over the whole year.

It is evident that possums spend a good deal of the time sitting and in fact resting. On an average males sit for 36% of the night and females for 44%. This sitting was not necessarily composed of numerous short bouts because both sexes, more especially females, spent periods of up to two hours resting at night. In one particular case, Jill spent two 1¾ hr periods of sitting separated by only a 0.3 hr period of moving about and feeding. Eventually I was above to recognise the onset of these longer rest periods and took advantage of them to have a rest from watching the possum. About 25% of the time is spent by both males and females in feeding in the trees.

Although primarily arboreal the brush-tail possum spends an appreciable time on the ground and the males twice as long (10%) as the females (5%). Not all of the time on the ground was spent in travelling because approximately half for both males and females was spent feeding. In fact brush-

tail possums are able to colonise relatively tree-less habitats. On Kangaroo Island they have taken to living in burrows (made by other species) (Finlayson 1963), and in New Zealand have become pasture feeders (Gilmore 1965; Harvie 1973).

In very general terms a definite nightly cycle of activity was recognisable. After emerging from its den in the evening a possum spends a short time, usually about ¼ hr., in the den tree grooming and just sitting, but with very little feeding. On leaving the den tree it spent a variable time on the ground, climbed one or two trees, then settled down for the first main feeding bout of the night, which may last for 1.5 to 2 hours. This was followed by a long rest period usually between about 10p.m. and 1.00a.m., and then by a second feeding bout. The furthest point from the den is reached within the first five hours of the night which is usually before the "midnight" rest period commences (Fig. 3.5). Between about 2.00 and 3.00a.m. the possum begins to move back towards its den tree, and it was at this time that much of the ground feeding occurred. Before entering its den the possum may sit in the canopy of the den tree, possibly with some desultory feeding and grooming.

The time spent in social interactions is very low and in this general sample was less than 2% for both males and females. This figure may be an underestimate for two reasons. First, the 1966 observations were made whilst keeping as far from the possum as possible. As a result some of the milder give-way interactions (Ch. 5.161) may have been missed. Secondly during courtship, interactions may increase considerably, but for the nights analysed here only one involved a consort relationship (Ch. 5.211). On this night Gus followed Gert for most of the night. They had five definable interactions with each other and Gert had one with another female, which meant that the time spent in interactions was 7.8% for Gert and 5.9% for Gus. The time they had spent together was 93.5% of Gert's time out of her den, and 84.7% of Gus'. For a short period during courtship the frequency of interactions may be high as discussed in Chapter 5.9, but generally the percentage of time spent in social interactions was low. In 18 of the 36

Table 3.7

A listing of the number of types of foods observed to be eaten by Trichosurus vulpecula during the course of field work. The frequency of ingestion of each food type is indicated in a qualitative way.

Food items	Frequency of eating
Eucalyptus territicornis (mature leaves, buds, young capsules)	Frequent - non-seasonal
E. hemiphloia (mature leaves, blossoms, buds, young capsules)	Frequent - non-seasonal
E. crebra (mature leaves)	Frequent - non-seasonal
(young leaves)	Rare
E. tesselaris (leaves)	Occasional
E. maculata (leaves)	Occasional
Amyema miquelii (a mistletoe) (flowers, buds)	Frequent - seasonal
Euroschinus falcatus (berries)	Seasonal
Angophora subvelutina (mainly young leaves, blossoms)	Frequent - seasonal
Tristania suaveoleus (leaves)	Occasional
Ficus sp. (leaves)	Rare
Ipomea cairica (a vine) (leaves)	Two observations
Mallotus philippinensis (leaves or fruit)	One observation
Acacia aulocacarpa (leaves)	Occasional
Lantana sp. (flowers)	One observation
Hawke moth larva	One observation
Cicada exuvium	One observation
Insect gall on branch of E. maculata	One observation
Agaric fungus	One observation (ground)

Continued on next page

Table 3.7 continued.

Food items	Frequency of eating
Probably eaten	
Grasses (assorted species)	(Ground)
Coranopus didymus (leaves)	(Ground)
Solanum nigrum (leaves)	(Ground)
Aphananthe philippinensis	(Ground)
Passiflora suberosa	May have killed male 6228 (Ground)
Available through man's activities	
Cattle feed (lucerne and millet mixture)	Frequent
Bean sprouts	One observation
Sprouting grain in cow pat	One observation (Ground)
Dried peas	One observation

Table 3.8

The amount of time spent feeding on particular foods during 36 nights of observation of individual possums. See Ch. 3.62 for method of analysing time spent feeding.

Food item	No. of nights eaten (36 max.)	Avg. time per night	Total time spent eating	Percent of total feeding
Eucalyptus territicornis	31	1.28	39.6	
E. hemiphloia	12	1.54	18.5	
E. crebra	16	.58	9.2	66%
E. tesselaris	3	.57	1.7	
E. maculata	1	.50	.5	
Angophora subvelutina	4	.58	2.3	
Tristania suaveolens	3	.63	1.9	
Ficus sp.	2	.30	.6	5%
Euroschinus falcatus	1	.90	.9	
Amyema miquelii	8	.81	6.5	6%
Ground feeding	35	.70	24.5	23%

Table 3.9

Frequency of tree species within the area of the six central individuals, and the relative time (expressed as 0.1 hr feeding units - see Ch. 3.62) spent feeding in each tree species. Tested for goodness of fit with "G" (Sokal and Rohlf 1969 Box 16.1).

Tree Species	No. of trees	Feeding units Observed	Expected
Eucalyptus terreticornis	253	396	206.80
E. crebra	204	92	166.75
E. tesselaris	130	17	106.26
E. haemiphloia	103	185	84.19
E. maculata	29	5	23.70
Angophora subvelutina	76	23	62.12
Tristania suaveolens	54	19	44.14
Casuarina cunninghamiana	13	0	10.63
Acacia aulococarpa	31	0	25.34
Ficus, Euroschinus etc.	27+	15	22.07
Total	920	752	752.00

G = 529.13, 9 d.f., p .005 +++

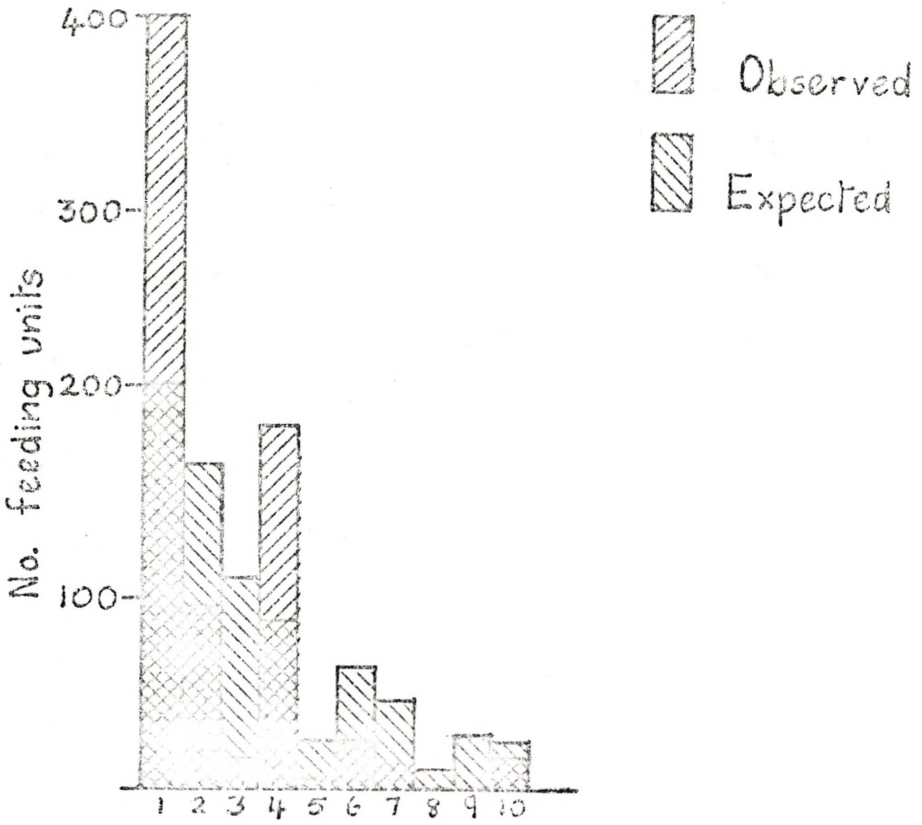


Figure 3.6 : Observed and expected feeding time in relation to tree species. Data are from Table 3.9 1 = E. terreticornis, 2 = E.crebra, 3 = E.tesselaris, 4 = E.haemiphloia, 5 = E.maculata, 6 = Angophora subvelutina, 7 = Tristania suaveolens, 8 = Casuarina cunninghamiana, 9 = Acacia aulocacarpa, 10 = Ficus, Eurosohinus etc.

nights analysed no interactions at all were recorded.

3.7 DIET

Observations throughout the study revealed that possums eat a wide variety of food types (Table 3.7). About half of these different food types were consumed on only one or two occasions. The bulk of the diet was made up of mature eucalyptus leaves supplemented with seasonally available foods such as the flowers and fruit of the mistletoe Amyema miquelii, the berries of Eucrosbinus falcatus, and the new leaves of Angophora subvelutina.

The predominance of Eucalyptus in the diet is reflected in the time spent feeding in the various tree species. Feeding on Eucalyptus, predominantly on the mature leaves, made up 66% of the total observed feeding time. Of this more than three-quarters is accounted for by feeding on E.terreticornis and E.hemiphloia (Table 3.8). The next most important type of feeding behaviour was ground feeding, which accounted for 23% of the total feeding time. Ground feeding involves the consumption of a variety of foods, few of which could be identified with certainity. Feeding from cattle troughs and on grain stored in sheds was included as ground feeding. Of the remaining 11% of the feeding time, 5% was spent feeding on the leaves, flowers etc. of four non-eucalypt tree species, and 6% on eating the flowers and fruit of mistletoe (Table 3.8).

The amount of time spent feeding in each species of tree differed significantly from the frequency of the species present in the home ranges of the six central individuals (Table 3.9). This suggests that possums preferentially selected certain species of tree as food sources. The most favoured species were E.terreticornis and E.hemiphloia, and there appeared to be a significant avoidance of E.tesselaris and to a lesser extent of E. crebra (Fig. 3.6). Seasonally there was a noticeable preference for the young leaves of Angophora subvelutina to the extent where one small tree was virtually defoliated. Possums were never observed to feed on Casuarina cunninghamiana at any time during the study. Even within the one species of tree there appeared to be a distinct preference for

certain trees. This was most obvious in the case of two E.terreticornis of the same size and 5m apart. One had numerous claw marks on the smooth bark and possums were regularly seen in it. The other was virtually free of claw marks on the bark and during the whole time of the study, possums were seen in it on only one or two occasions. Individual trees may vary in their palatability, or else there may be a social basis for such preference of certain trees.

3.8 INJURIES AND FALLS

The most noticeable and presumably one of the more serious injuries was to the eye. Five possums (1 female, and 4 males) were observed with eye injuries. Two of these were permanent. Female Dim-right-eye had an opaque lens to her right eye, and an unknown male had the eye lid sealed over what appeared to be an empty eye socket. Donald received a scratched cornea during a series of fights with other males when preventing them from mating with Lesley. Scar tissue formed on the cornea and this reduced the brightness of the eye reflection in the spotlight by more than half. Six months later his eye was still very dim, but 15 months after he was injured his eye reflection was almost back to normal. Male 33 also had a dim eye, and Male 32 received a deep vertical scratch across the eye lids, which caused them to stick together for a few days but did not damage the eye itself.

Possums are probably prone to receiving eye injuries when fighting with each other. Other injuries seen were minor, such as a scratched ear and a scratched paw following fighting, and numerous small scratches on a female's shoulders from carrying a joey on her back.

One female did received a substantial injury during the study. She was seen with a fresh deep wound on the small of her back about 1 cm in diameter. The wound looked as though it had been made by the end of a sharp stick or possibly a bird's bill. When it healed a polyp of proud flesh about 0.5cm long remained protruding.

The possum is a careful and sure climber, but all the same it did fall from time to time. Thirteen falls were observed. Six of the falling

possums were males who fell from a branch during an interaction with another male (4 obs) or with a female (1 ob), and the last when a young male was still flustered after being chased by an older male several times.

A female was observed to fall twice and on both occasions she was carrying a joey on her back. In one Jill was negotiating to enter her den when the weight of the joey apparently caused her to lose her grip with her hind feet and to somersault backwards. Jess was laboriously climbing the vertical trunk with her joey clinging to her back, when she suddenly fell to the ground. The tree was shedding its bark and the long loose strips of bark may have been responsible for her fall. In both falls the joey remained clinging to its mother's back even following impact with the ground.

Juveniles were observed falling five times. In three it was the result of supplanting activity by a female, and the young possum, cornered at the end of a branch, fell during its efforts to get past the female. In the other two, the falls were apparently through inexperience at climbing. On several other occasions young possums were observed to lose their footing without falling.

The possums sometimes appeared dazed after a fall, especially the females carrying joeys, but otherwise they seemed to suffer no ill effects.

3.9 INTERACTIONS WITH OTHER SPECIES

3.91 Other Arboreal Mammals

Four other arboreal mamals were observed in the study area, but none in such large number as T.vulpecula as shown by the mean number seen per census transect (Table 3.10).

Two of these, the squirrel glider, Petaurus norfolcensis, and the greater glider Schoinobates volans occurred in the open forest so had a similar distribution to Trichosurus vulpecula, and the number seen is comparable, except that the squirrel glider is smaller and more active so presumably more difficult to spot. Schoinobates were consistently in the area until the end of October 1965, but absent for two years as the next sighting was in November 1967 when one was seen, and it was the last

sighting for the rest of the study. P.norfolcensis was seen throughout the study period, usually one or two individuals, but twice during a census four were seen.

Table 3.10

The number of arboreal mammals observed during each of 39 census transects at Moggill Farm.

	Mean	S.D.	S.E.	Range
Trichosurus vulpecula	23.72	6.36	1.02	15-39
Schoinobates volans	0.49	0.75	0.12	0-2
Petaurus norfolcensis	1.10	0.93	0.15	0-4
Trichosurus caninus	0.74	1.01	0.16	0-3
Pseudocheirus peregrinus	0.54	0.81	0.13	0-3

The other two species, the short-eared brush-tail Trichosurus caninus and the common ring-tail possum Pseudocheirus peregrinus were confined to the riverine vine forest and to a lesser extent the mangrove fringe. T.caninus was observed no further than 10m from this type of vegetation, but once a P.peregrinus was seen in the middle of the study area in open forest. Because of their habitat restrictions, numbers observed during censuses which only touched the fringes of these habitats, are not comparable.

Both P.norfolcensis and S.volans use pre-existing cavities in the eucalypt trees as day time dens in the same manner as T.vulpecula, so there is the possibility of interspecific competition for these dens. P.norfolcensis is much smaller in size than T.vulpecula and can therefore utilise cavities too small for the brush-tail possum. Schoinobates on the other hand is of a similar size to T.vulpecula. Only one dispute over den occupancy was observed. A Schoinobates, seen for the first time for about two years, was sitting outside a den about 1 hr before dawn. The den was one that had been used by the adult female Gwen the previous day. About an hour later Gwen approached her den and the glider hurriedly vacated it when Gwen was 1-2m away from the entrance. They sat looking

at each other, then Gwen slowly moved towards the glider which moved away and Gwen entered the den. Soon afterwards the glider left the tree without making any attempt to re-enter the den.

Trichosurus caninus also uses hollows as dens, but there tends to be a habitat separation of the two species. Pseudocheirus peregrinus builds a nest amongst dense vegetation. (Thompson and Owen 1964).

Interspecific interactions were rare. The only other interactions with Schoinobates also took place in a den tree at dawn. A Schoinobates peered out of a den it had entered, when a young Trichosurus vulpecula began to climb the tree. The glider withdrew back into the den, and the young possum took no apparent notice of it.

Only once were a Trichosurus vulpecula and a Trichosurus caninus seen in the vicinity of each other. Both were feeding in the same tree, no more than 5m apart at one stage, but both appeared to completely ignore each other. The T.vulpecula was an adult male, and the T.caninus an adult female with a bulging pouch.

Two interactions between Trichosurus vulpecula and Petaurus norfolcensis were recorded. In one a glider landed on a tree trunk 1m above an adult male possum. They gazed at each other for a moment then the glider spun round and went higher up the tree. In the other a female possum and a Glider came out of their respective dens about 3m apart on the same branch. The possum gazed in the direction of the glider then ran along the branch towards the trunk, which was also towards the glider. The glider ducked back into its den when the possum, who took no apparent notice of the glider, approached and without pausing passed over the entrance to the glider's den. After she had passed the glider came out of its den again, ran to the end of the branch and took off.

3.92 Terrestrial Mammals

The only native terrestrial mammal in the study area was the short nosed bandicoot (Isoodon macrourus), and no interactions were observed between it and the brush-tail possum. All others were introduced species.

Domestic dogs (Canis familiaris) were occasionally seen in the area

and once a female was seen chased up a tree by two dogs. On two other occasions a female (the same one) responded to a barking dog in the distance by climbing into a tree, or climbing higher in a tree. Dingoes were not seen or heard in the area.

A fox (Vulpes vulpes) was once seen in the study area but no interactions were observed with the possums.

Domestic cats (Felis catus) were common round the feed sheds in the S.W. corner of the study area, and a number of interactions were observed. Twice a possum low in a tree peered down at a cat on the ground, and once chattered, possibly in response to the cat. Five interactions took place on the ground and in all five it was the possum who gave-way. In one, Jack came within 5m of a white cat, sat up in the upright alert, then bounded away. He circled round the cat keeping 5-6m from it and frequently in the upright alert. The cat remained crouched on the ground. Fifteen minutes later another male approached within half a metre of the same cat, which was sitting. He stretched his nose towards the cat then circled round to climb a tree near by. In a third observation a possum stopped when 3m from the same white cat, which casually walked towards the possum. The possum made an alarm dash onto a tree and looked towards the cat which had stopped. The possum then jumped to the ground and walked straight towards the cat, coming within 1m before jumping aside into long wet grass. In a fourth observation a female stopped to look at a cat 4m away and gave-way when the cat walked towards it. Only once did a cat actually chase a possum, who sprang onto a nearby tree, but it was a young cat and the chase possibly playful.

Whilst cats are known to prey on possums occasionally, the interactions above suggest that this is not a regular feature, as the possums showed only mild alarm towards cats, although in one instance an alarm chatter may have been a possible response. Dogs, on the other hand, especially dingoes in the natural habitat, probably do constitute a significant predator to the possum which spends a relatively high proportion of its time on the ground.

Cows and horses were treated with indifference unless they made a sudden noise or movement in which case the possum made an alarm dash.

3.93 Birds

Three species of birds were known to use holes, suitable as possum dens, as nests. These were the kookaburra (Dacelo gigas), dollar bird (Eurystomus orientalis), and pale-headed rosella (Platycercus adscitus).

A pair of pale-headed rosellas were observed nesting in a cavity formerly used as a possum den, but it was not known whether the birds displaced the possums from the den.

Twice a dollar bird used a cavity frequently used by possums as a den, suggesting that the dollar bird had in fact displaced the possum. The only actual interaction observed took place when a possum approached a den tree before dawn and disturbed a dollar bird sitting at the entrance of a den. The bird flew to a nearby branch with a squawk and the possum continued past the den. The bird made 3 to 4 more squawks, which coincided with movements made by the possum, but made no attempt to attack it.

Kookaburras, being larger and with a large powerful bill, may compete more for hollows used by possums than the above two species of bird. The following interactions were observed. A young female possum had emerged from her den just before dusk and was sitting by the entrance when a kookaburra landed on the trunk beside her. This made the possum hurriedly climb higher. One year kookaburras and possums were seen sharing a den. At dusk on 7th November 1968 two kookaburras were mating on a branch by the entrance of a den frequently used by possums, though not that particular day. On the 12th November 1968 Gwen approached a den to enter it just before dawn but drew her head back suddenly, possibly because pecked by a kookaburra sitting in the entrance. Gwen then moved very slowly towards the bird which gave one peck causing the possum to draw back. Gwen moved towards the den again and slowly pushed past the bird which pecked at her twice but did not prevent her entering the den. The kookaburra remained at the den entrance while Gwen's juvenile sat just over the den entrance looking at the bird. However, it moved towards the bird which appeared to

peck the juvenile on the nose causing it to draw back and to sit gazing at the bird. Two minutes later the juvenile again approached the bird which gave one to two pecks, but instead of withdrawing the young possum turned its head so the crown was towards the bird's bill and slowly pushed past the bird. The kookaburra gave one or two more pecks but desisted and merely moved to one side as the possum pushed past.

A female possum reacted to the distress calls of a juvenile mudlark (Grallina cyanoleuca) by approaching it, possibly mistaking the calls as distress calls made by her joey (see Ch. 5.6146).

CHAPTER 4

C O M M U N I C A T I O N

4.1 AUDITORY BEHAVIOUR

4.11 Introduction

This section contains a descriptive catalogue, at the syntactical level, of sounds produced by the possum and which could be recognised either by ear or from electronic analysis of tape recordings. Following the catalogue the functional significance or meanings, at the pragmatic level, of sounds is inferred from their temporal distribution, their context, and from the response of other individuals. Description and functional considerations of the sound are separated for two reasons. Firstly the initial exclusively syntactical approach as suggested by Marler (1956) avoids any assumptions as to whether a sound has a communicative function, also it allows a more flexible interpretation of function in that the same sound in different contexts may have a different meaning as pointed out by Smith (1965). Secondly both the descriptive and functional data were collected concurrently with the logical result that more sounds were described than recognised when I started collecting the functional data.

All the basic sounds of the possum have been recognised by previous workers (Jones 1921, Fleay 1947, Kean 1967), but descriptions of the sounds have been brief and no systematic functional analysis made. This section looks at auditory behaviour in more detail.

4.12 Methods

During field observations all calls were noted and also whenever possible their context and the response of other individuals.

Tape recordings were made with a Uher 4000-S portable tape recorder (frequency range, 40-20,000 khps manufacturers specifications) at a speed of 19cm/sec, and a Grampian microphone, Type DP4 (frequency response 50-15,000 khps manufacturers specification). For field recordings a Grampian 60.8 cm parabolic reflector was also used.

The tape recordings were analysed with a Kay Electric sonograph

(Model R 662 B) using the F1-1 shaping switch and the wide bandpass filter (300 khps resolution). Amplitude patterns were examined on a Tetronix Type 502A Dual-beam Oscillograph. Both the sonograph and the oscillograph were used in conjunction with an Akai Terecorder tape recorder (frequency range 50-12,000 khps manufacturers specification). Temporal analysis of long bouts of recorded calls was done with an Esterline Angus Event Recorder.

Phonetic descriptions of sound follow the pronunciation given in the Concise Oxford Dictionary.

4.13 Definition of Terms

The following terms are used in the description of sonogram and oscillogram pictures of the sounds.

Unit "The unit is the basic element of a sound or call and is represented as a continuous tracing along the temporal axis of the sonogram." (Struhsaker 1967). Although it is usually easy to distinguish units, difficulties do arise when faint traces exist between apparent units. These connecting traces may be underemphasised because a sonograph is not very sensitive to faint sound (Fant 1956). Alternatively dial settings of the sonograph can noticeably alter the intensity of the connecting traces. Where the difference in intensity between the apparent units and the connecting trace is pronounced, the connecting trace is usually ignored, but where there is some doubt the author should clearly indicate his decision. For example it is impossible to tell from Struhsaker's (1967) description of the vervet 'Intergroup Chutter' which is a unit and which a phrase, unless "one pays $2.25". The unit is equivalent to a note in bird song (Borror 1967) and to the sound between breath stops in human speech (Cherry 1957).

Phrase "The phrase is a group of units that is separated from other similar groups by a time interval greater than any time interval separating the units within a phrase." (Struhsaker 1967).

This is a well established term in the description of bird calls (e.g. Borror 1967).

Bout "A bout is a grouping of one or more phrases separated

from other similar groupings by a time interval greater than that separating any of the phrases of a bout." (Struhsaker 1967).

This is equivalent to song in bird terminology (Borror 1967).

Nontonal unit. "A nontonal unit is composed of sound that is more or less continuously developed over a wide range of frequencies." (Struhsaker 1967). This has also been called 'noise' (Andrew 1963) and 'harsh noise' (Rowell and Hinde 1962).

Struhsaker's term is preferred because in acoustics noise is often defined as 'undesired sound' (Randall 1951).

Tonal Unit "A tonal unit is composed of sound characterized by one or more relatively narrow frequency bands and has been referred to as 'clear calls' by Rowell and Hinde (1962) and 'sound' by Andrew (1963). Units with harmonic structure are included in the category." (Struhsaker 1967).

Formant A formant is a region of maximum resonance which appears as a dark horizontal band on a sonogram. The number and spacing of formants depends on the characteristics of the resonating chambers of the vocal tract, and they should not be confused with harmonics (see Cherry 1957, Stevens and House 1961, and Ladefoged and Broadbent 1967). A formant is identified by its median frequency (Fant 1956).

Andrews (1963) defined and used descriptive terms such as 'vocal fry', 'crackle', 'grunts', 'moans', and 'twitters'. The only one used in this study is the grunt which he defined as a short call with a low fundamental.

General terms used to describe the amplitude patterns within a unit are; (1) A smooth amplitude pattern is one that gradually increases or decreases in amplitude; (2) a rough amplitude pattern is one that has pronounced amplitude peaks following rapidly one after the other in the same unit, the amplitude peaks appearing as distinct vertical striations on a sonogram and as steep fronted peaks on an oscillogram; and (3) a pulse which is a single peak of sound that fades rapidly.

4.14 Description of Sounds

The classification of vocalisations is initially based on whether

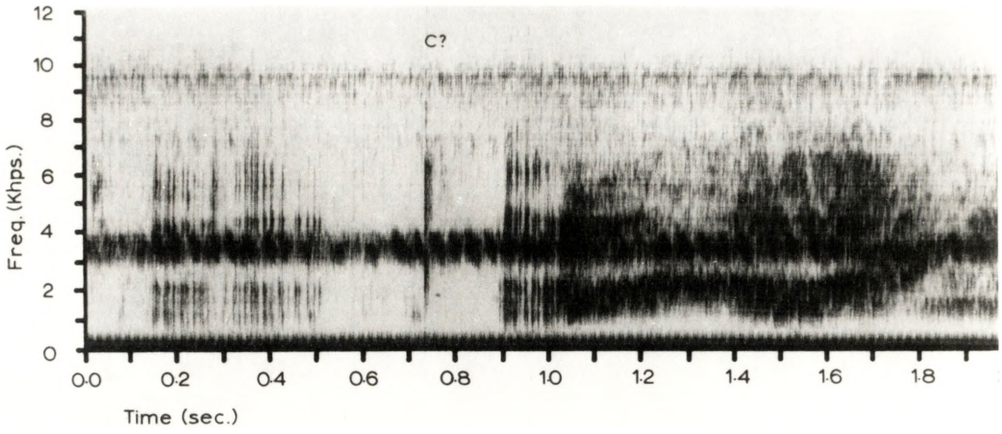


Figure 4.1: Sonogram of a growl (0.15 - 0.5 sec) followed by a growl-screech (0.9 - end). A click (?) may also be present. Frequency is vertical axis, time on horizontal axis.

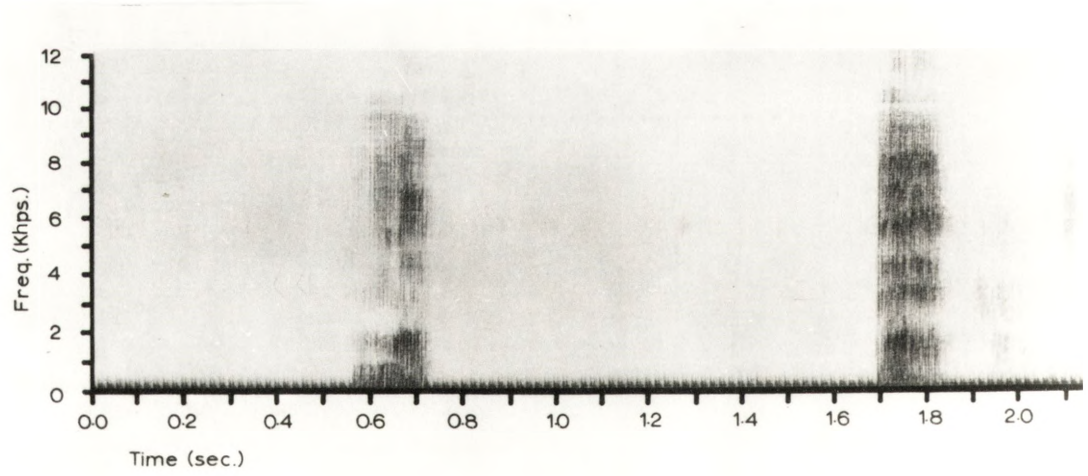


Figure 4.2: Sonogram of two grunts. Note trace right to base line. Numerous faint formants are present.

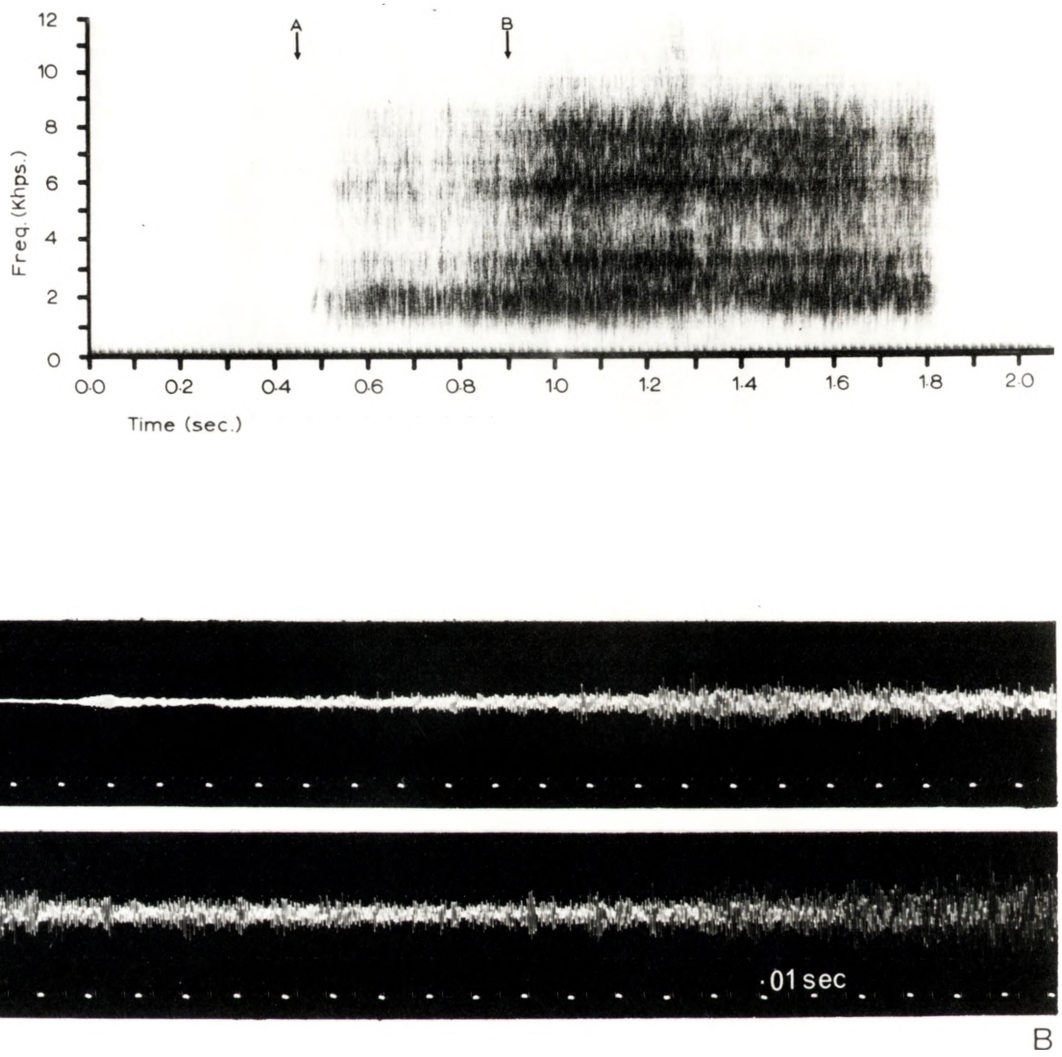
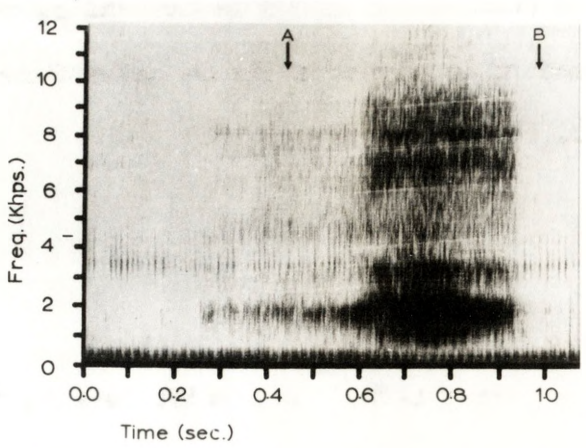


Figure 4.3: Sonogram - A hiss with formants at 1.75, 3.5, 5.75 and 7.75 Kh. A tonal sliver is present at the beginning of the hiss at 0.5 sec on the time scale.

Oscillogram - A segment of the hiss shown on the above sonogram between A and B. Note smooth amplitude pattern and tonal sliver 0.04 sec from A. Trace runs from left to right.



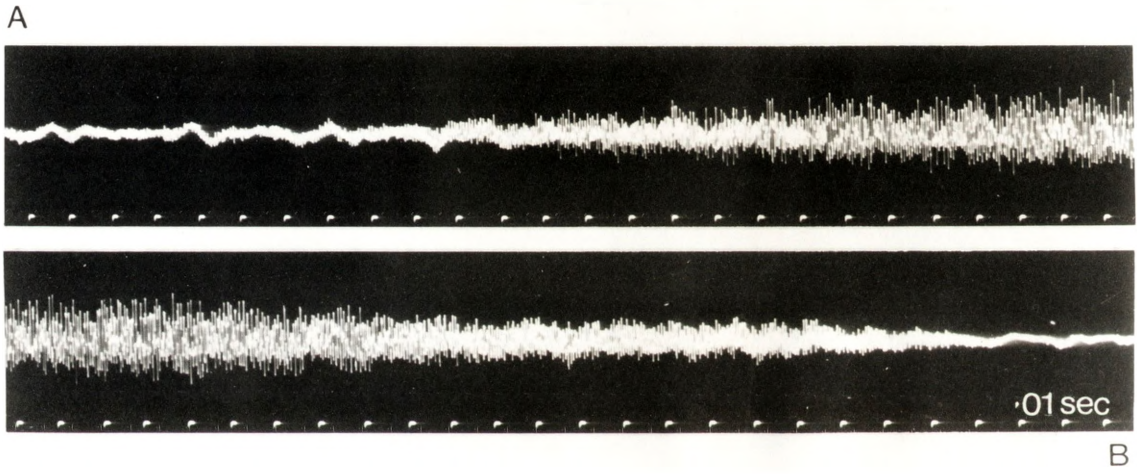


Figure 4.4: Sonogram - A hiss with the lowest formant (1.75 Kh) emphasised.

Oscillogram - The above hiss between A and B. Note smooth amplitude pattern and gradual rise and fall of amplitude from beginning to end.

a call is phrased, than on whether it is a simple or complex call. A simple call is one that cannot be subdivided into discrete calls, whereas a complex call is one that is composed of two or more simple calls fused to form a recognisably distinct call.

4.141 Non-phrased

4.1411 Simple

4.14111 Growl

The growl is a deep guttural call which is very rough in quality, and can be partially imitated by hawking to clear one's throat but without raising the pitch and by keeping one's mouth almost closed. The rough quality of the call is clearly shown on a sonogram (Fig. 4.1) as vertical striations approximately 0.014 sec apart. It carried from 50-100m.

4.14112 Grunt

The grunt is a short low pitched explosive call that can be partially imitated by a short chesty cough. It is much shorter than the growl and on a sonogram can be distinguished from all other calls by the very difinite trace below 1.0 Kh which goes right to the base line (Fig. 4.2). Several faint formants are present.

4.14113 Hiss

The hiss is a low intensity call that can be imitated by giving a fricative unvoiced Heeeeeee. As the call is made the possum has its mouth partly open. This is probably the same call described by Kean (1967) as a low Aaaah sound.

A sonogram of a typical hiss (Fig. 4.3) shows a broad frequency range with four faint formants. A variation on this type of hiss is shown in which the lowest formant, 1.75 Kh, is emphasised (Fig. 4.4). The amplitude pattern of oscillograms is smooth. (Figs. 4.3, 4.4).

Figure 3 has a tonal sliver right at the beginning of the call caused by a faint whistle as the possum exhaled.

4.14114 Screech

The screech is a fricative unvoiced call similar to the hiss, but of much greater intensity and which may carry for over 100m. This is the

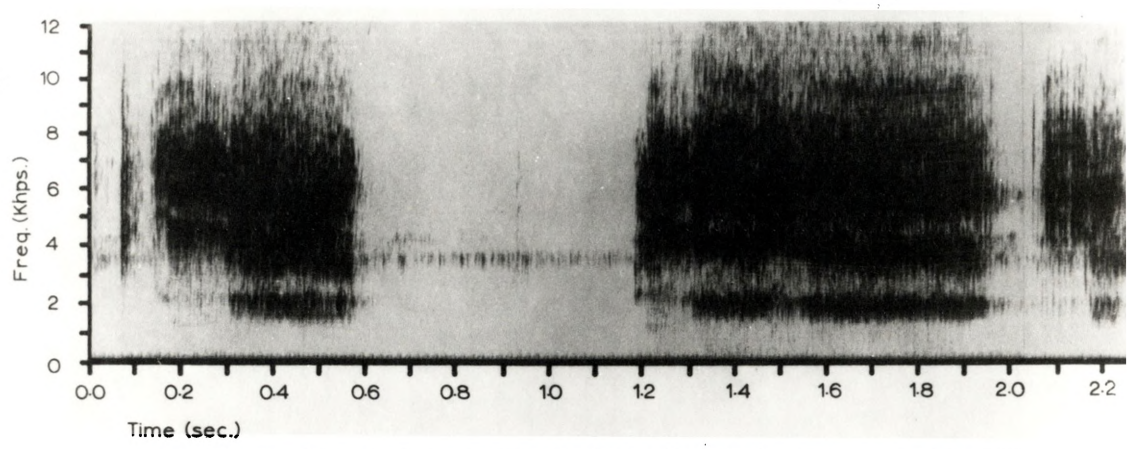


Figure 4.5: Sonogram of a series of screeches. Formants at 2.0, 4.0 and 5.5 Kh.

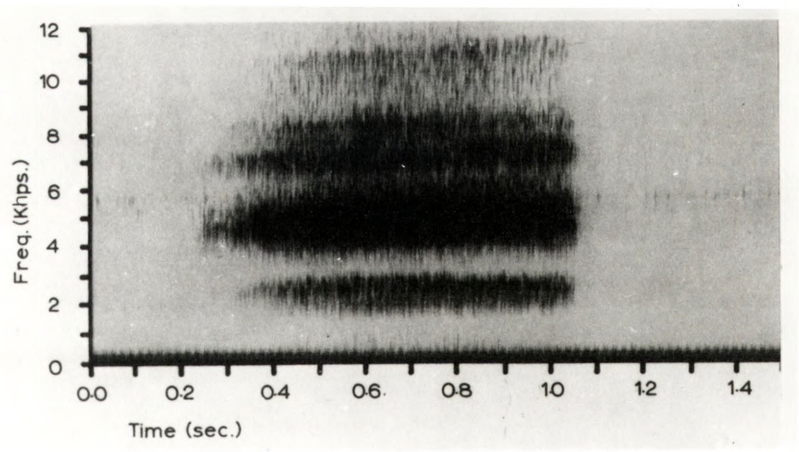


Figure 4.6: Sonogram of a screech. Formants at 2.5, 5.0 and 7.0 Kh, with the 5.0 Kh formant emphasised.

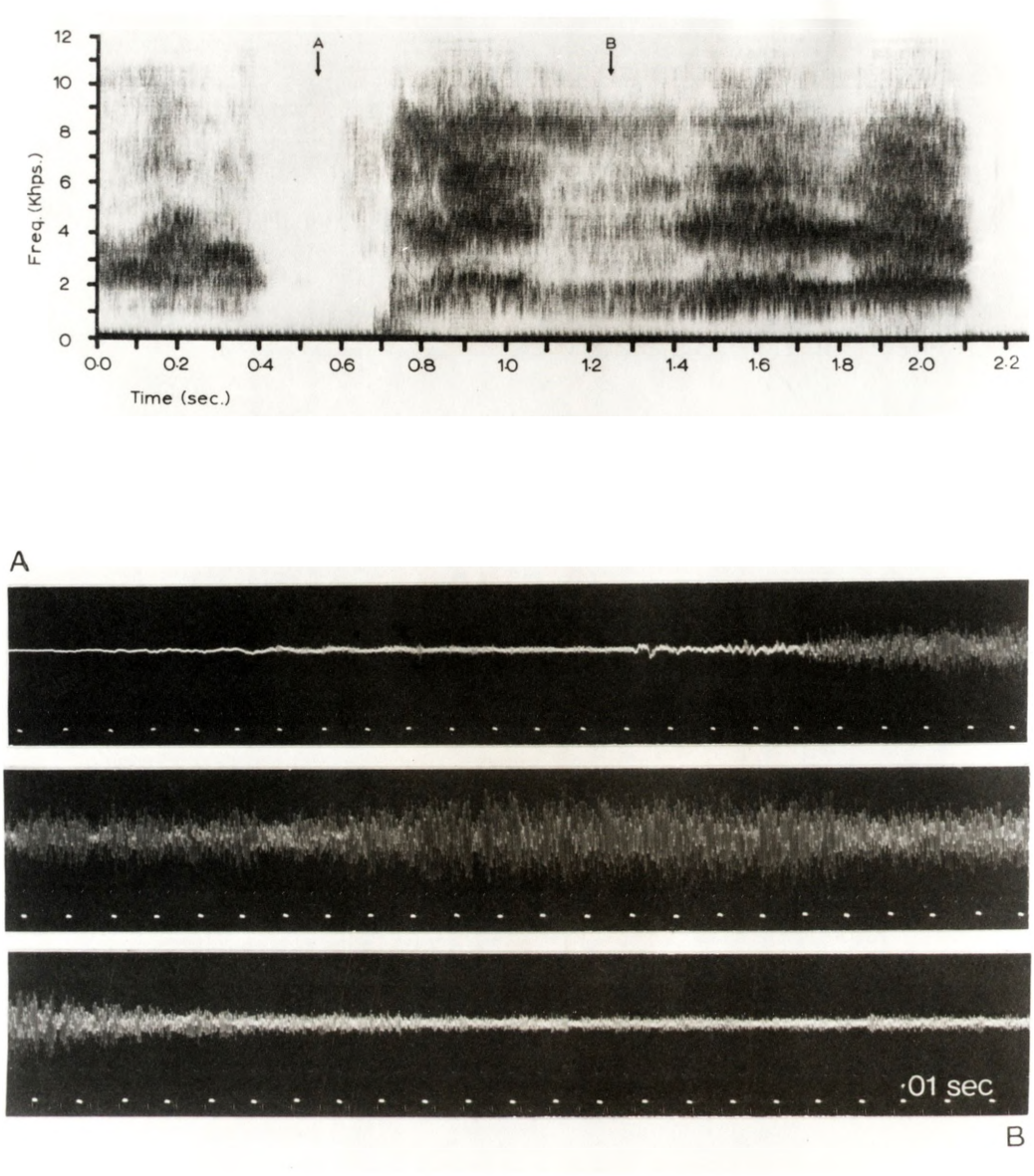
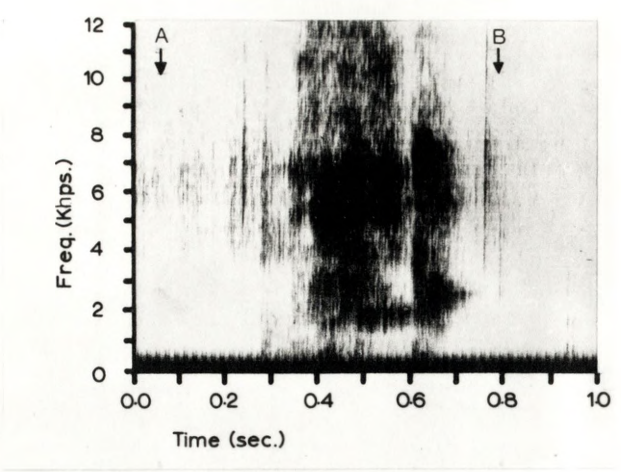


Figure 4.7: Sonogram - a long screech (0.72 to 2.1 sec) with fluctuating amplitudes and formants. A grunt (0.6 to 0.72 sec) occurs at the beginning.

Oscillogram - the above grunt-screech between A and B.



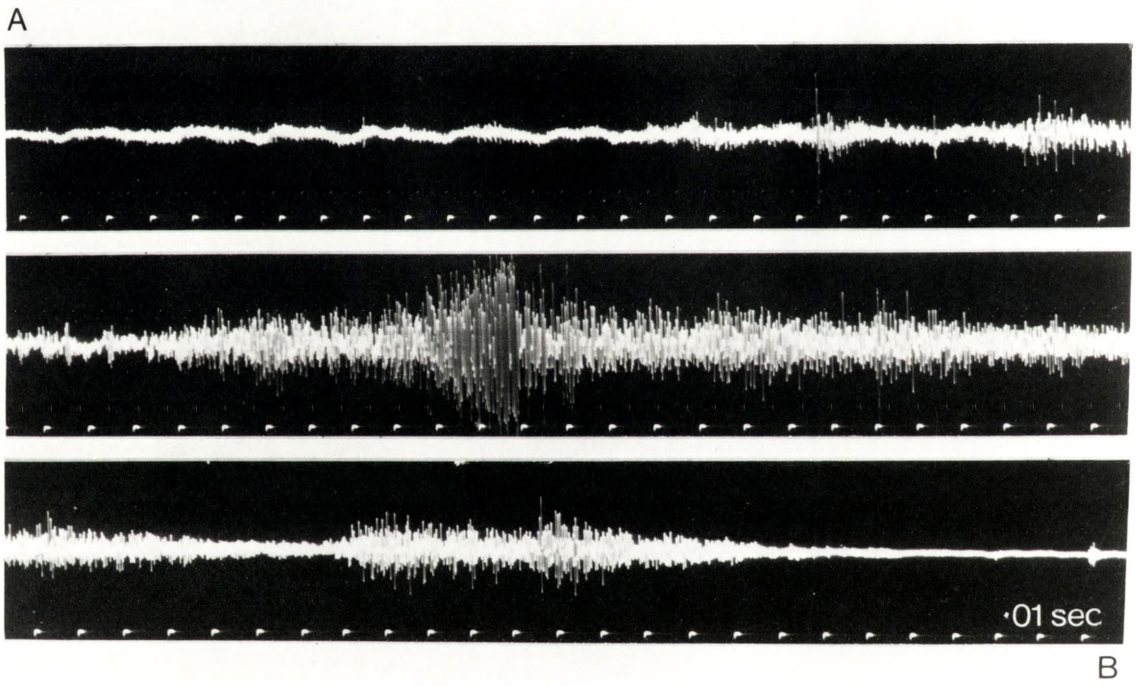


Figure 4.8: Sonogram - a screech with two sub-units.
Note slight rise in frequency of formants
of second sub-unit.

Oscillogram - above screech between A and B.
Note sudden amplitude burst in middle of trace.

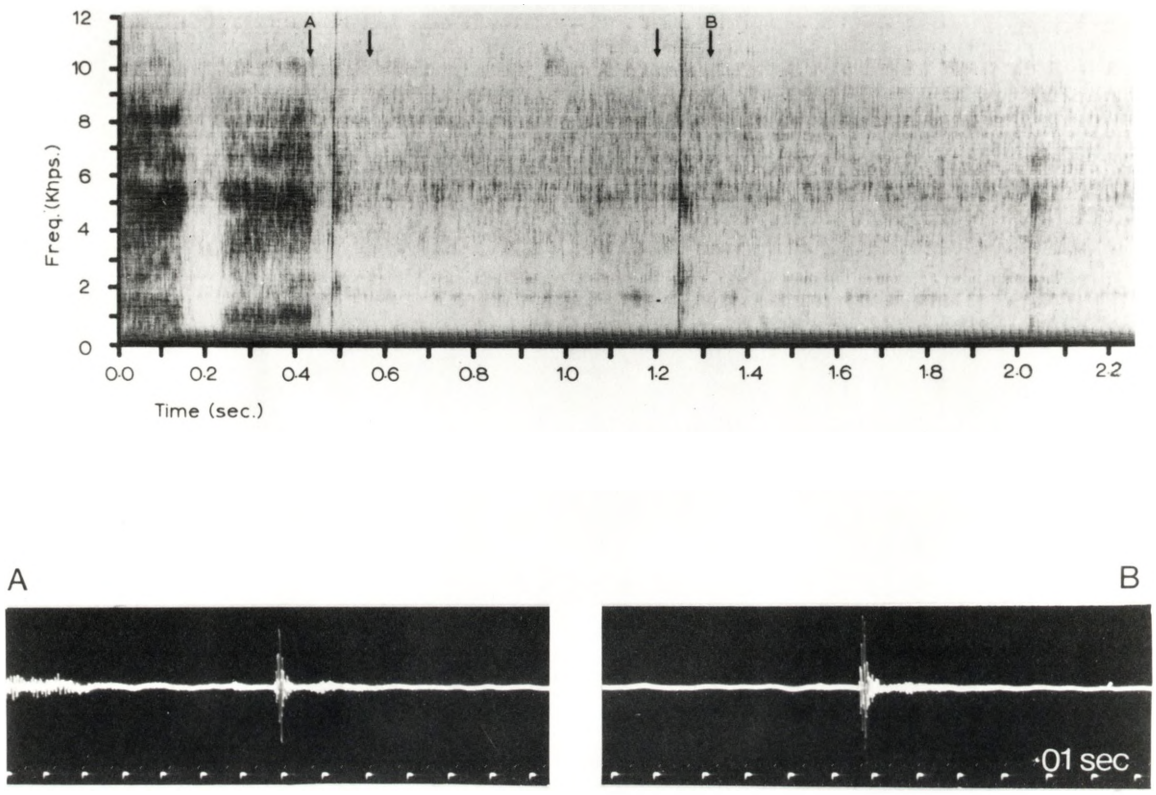


Figure 4.9: Sonogram - three clicks at 0.48, 1.25 and 2.03 sec. Note thin clear trace to 12 Kh in first two clicks.

Oscillogram - first and second clicks shown on sonogram.

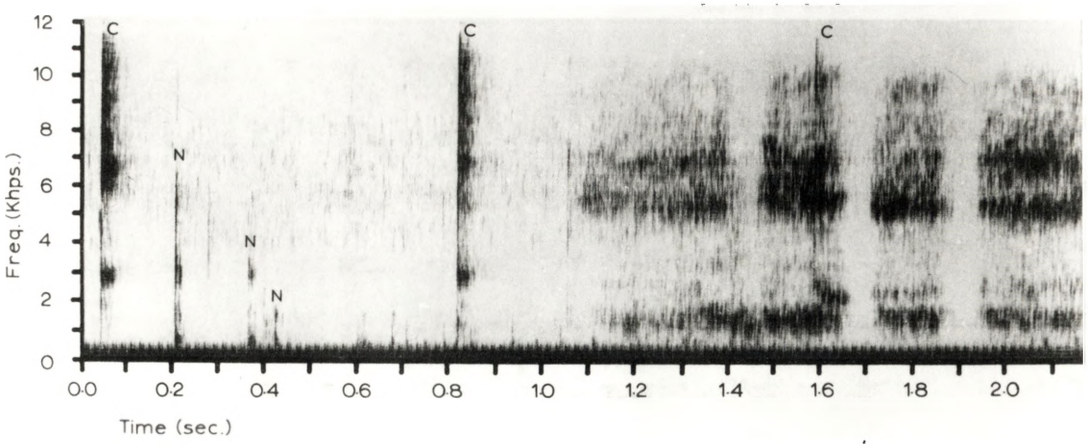


Figure 4.10: Sonogram of three clicks (C), the third click is superimposed on a unit of another call (shook-shook) made by the same animal. Machine noise (N) is prese

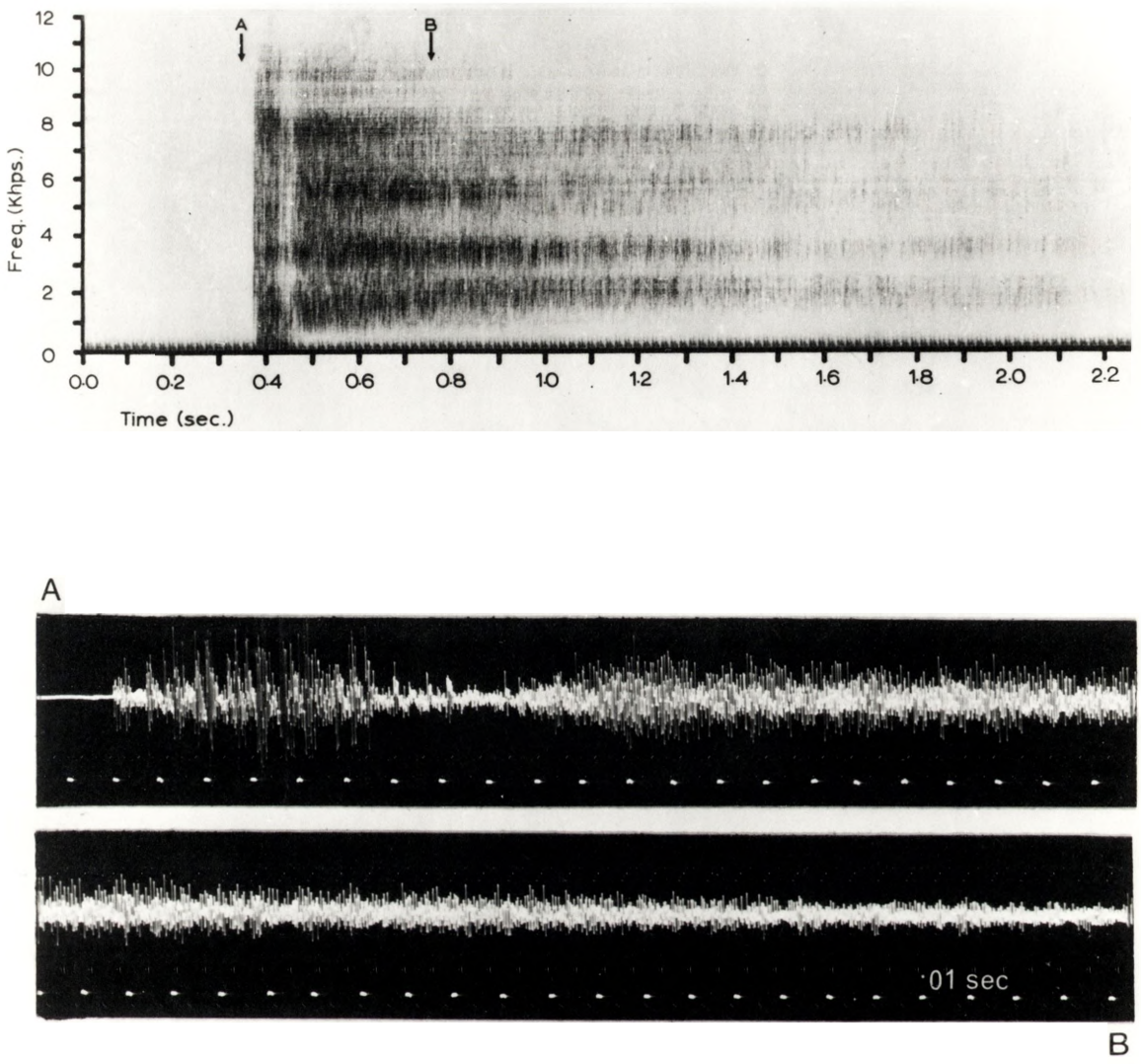


Figure 4.11: Sonogram - a grunt-screech-hiss. The grunt (0.39 to 0.45 sec) has the trace to the base line. The screech gradually fades into the hiss.

Oscillogram - the above grunt-screech-hiss between A and B. Note rougher amplitude pattern of the grunt.

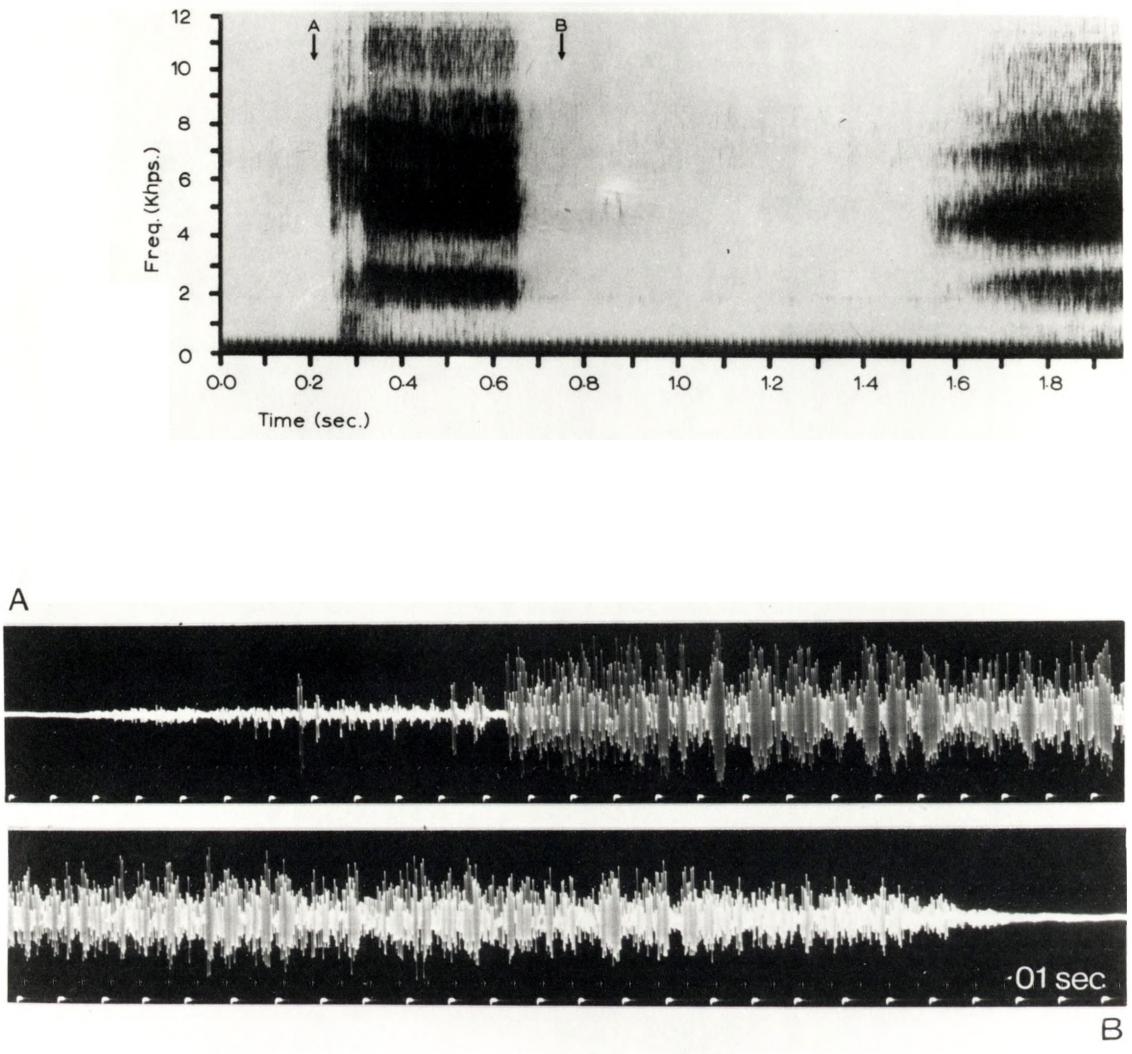
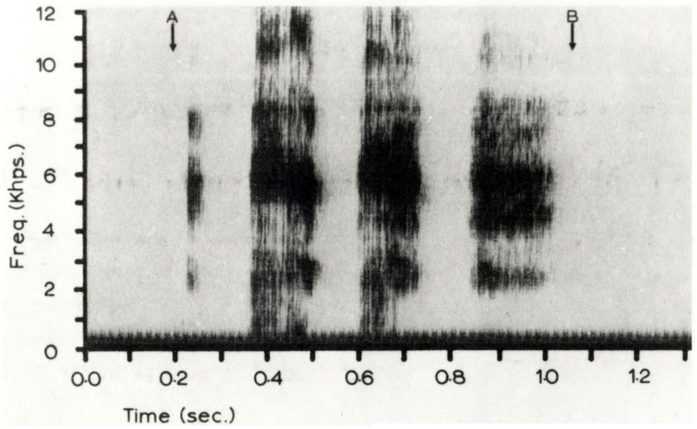


Figure 4.12: Sonogram - a grunt-screech followed by the beginning of a screech. The grunt segment (0.25 to 0.32 sec) is quite distinct in structure from the screech segment

Oscillogram - trace of the above grunt-screech between A and B. Note the sudden increase in amplitude from the grunt to the screech, and the comparatively rough amplitude pattern of the screech.



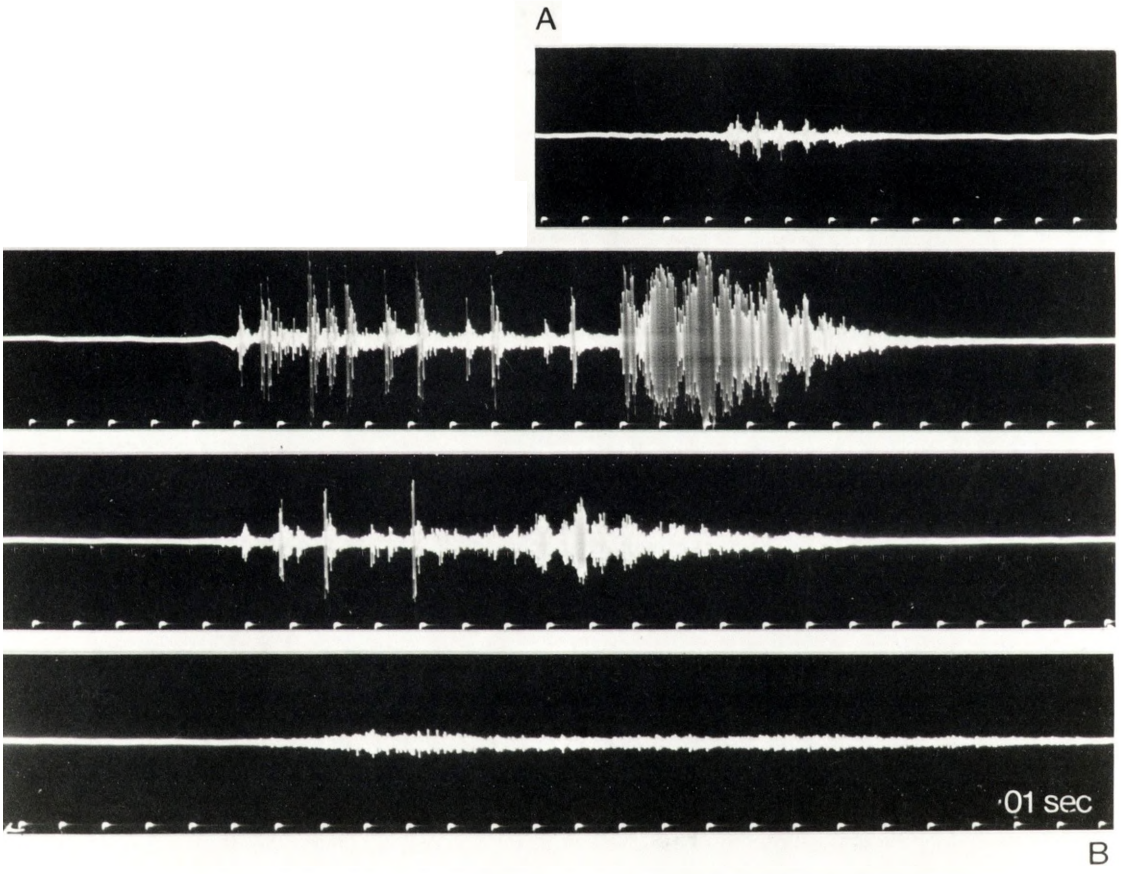


Figure 4.13: Sonogram - a brief growl unit followed by 2 grunt-screeches and a screech.

Oscillogram - trace of the above 4 units. Note rough amplitude pattern of grunt section of the first grunt-screech unit, and smooth pattern of the screech unit.

Complex unphrased calls are formed by the fusion of four of the simple calls - the grunt, growl, hiss, and screech.

A grunt may frequently occur at the beginning of a screech to form a grunt-screech. A variation in which the grunt was higher pitched was often referred to as a K-screech in the field notes because of its explosive beginning. On a sonogram (Figs. 4.11, 4.12) the grunt can be distinguished from the screech by its trace below 1.0 Kh. The amplitude pattern of the grunt varies from being similar though slightly rougher than the screech (Fig. 4.11) to one which is extremely rough (Fig. 4.13), and which begins to show as distinct vertical striations on the sonogram. A screech which is attached to a grunt may also show a comparatively rough amplitude pattern (Fig. 4.12). The amplitude pattern in Figure 4.13 is very similar to that of a growl, for which there are no adequate oscillograms because of background noise. There may in fact be a graded series of grunts leading through to a growl, and although a grunt can usually be distinguished by its trace below 1.0 Kh on a sonograph even this is sometimes difficult.

A growl, with pronounced vertical striations and a lack of a trace below 1.0Kh on the sonogram, precedes a long screech in Figure 4.1 to give a growl-screech.

Similarly a hiss may grade into a screech to give a hiss-screech or visa versa to give a screech-hiss. Unlike the grunt-screech and growl-screech there is no sharp demarcation between the hiss and the screech.

Combinations of simple calls can go a step further with three forming a complex call such as the grunt-screech-hiss (Fig. 4.11).

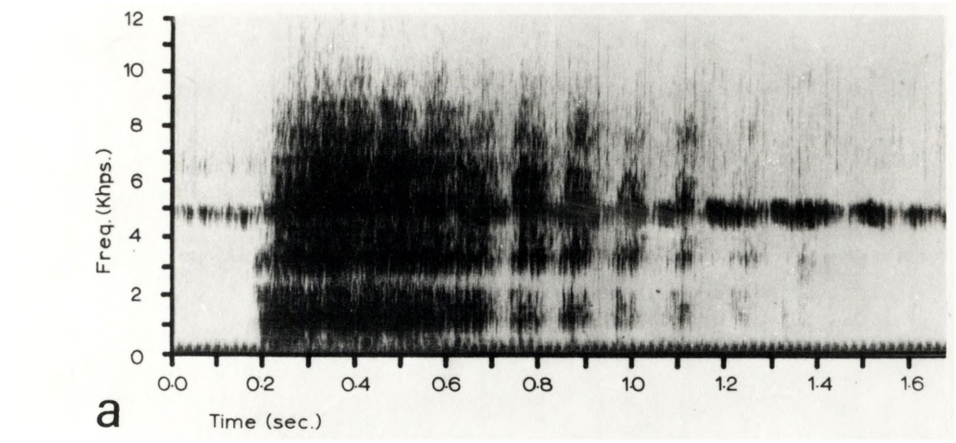
The click, although it may occur at the same time as another call, does not combine with one to form a definite type.

4.142 Phrased

4.1421 Simple

4.14211 Chatter

The chatter is a loud rough call that carries over distances of 100-200m, and is the call discribed by Kean (1967) as ".....a uvular Wuh-uh-uh-uh-uh."



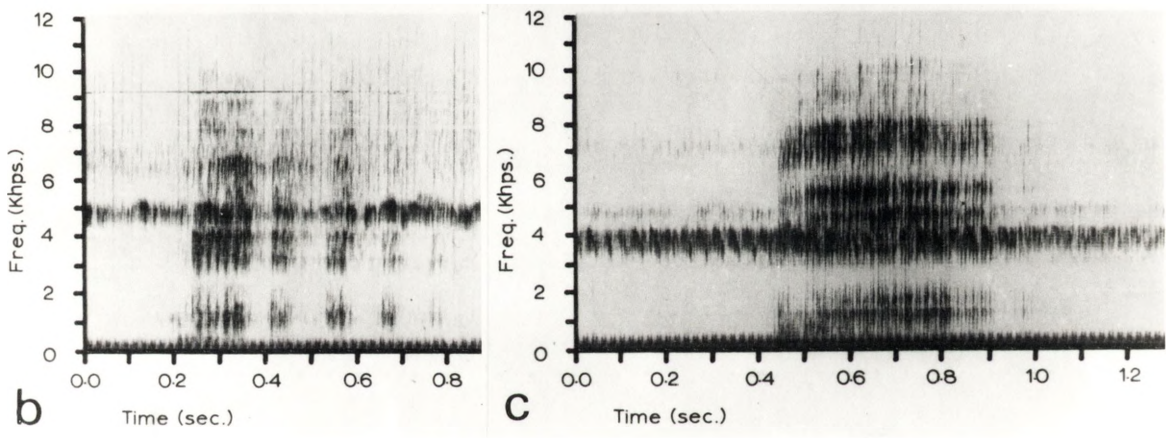


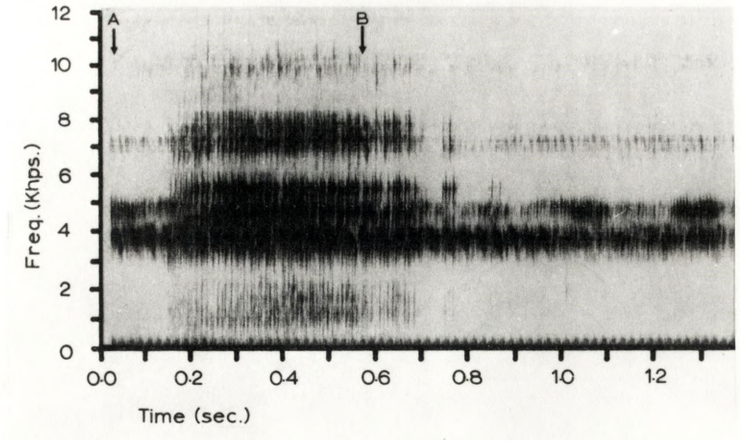
Figure 4.14: a) A chatter phrase with a long initial unit followed by 6 fading shorter units, the last at 1.36 sec.

b) Chatter phrase with a shorter initial unit followed by 4 shorter units.

c) Chatter phrase consisting of a long initial unit followed by one very faint short unit at 0.98 sec.

Note vertical striations particularly in initial units of b and c.

Ignore orthopteran background noise at 5 Kh.



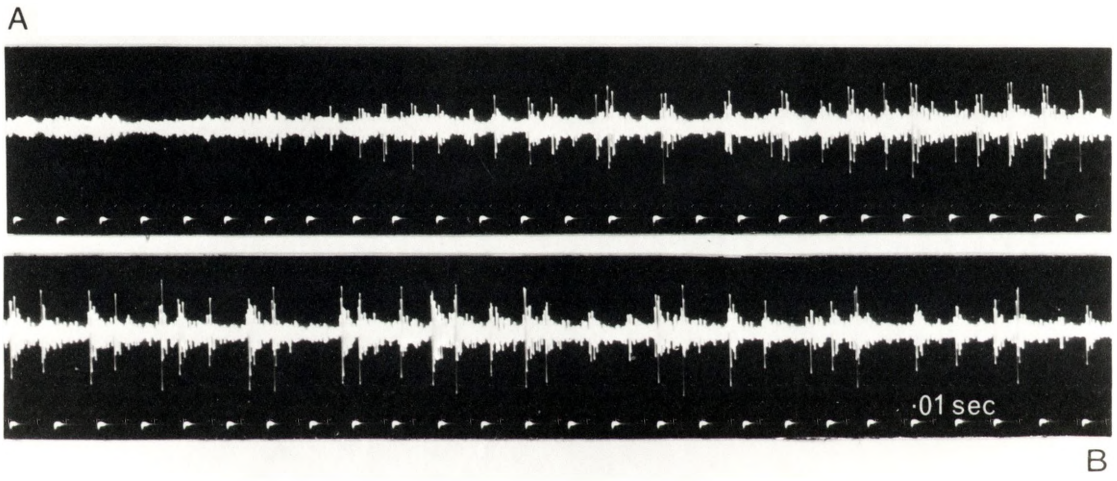
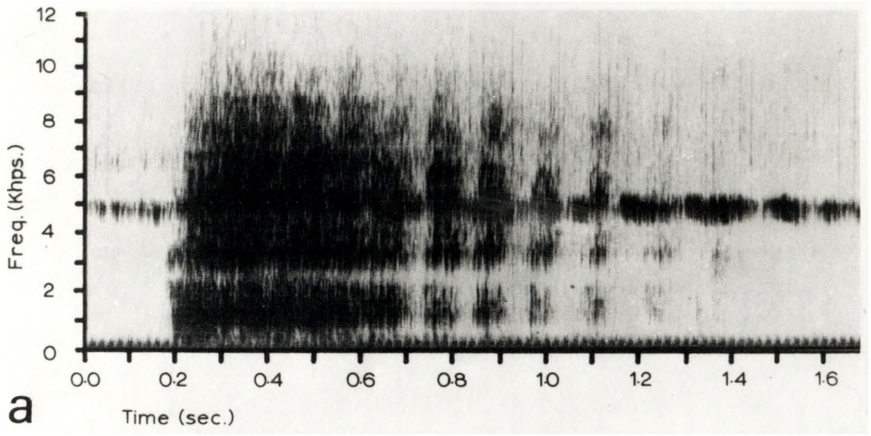


Figure 4.15: Sonogram - three unit chatter phrase (2nd unit at 0.75, 3rd unit at 0.85 sec). Ignore orthopteran background noise 3.5 to 5.0 Kh.

Oscillogram - trace of above sonogram between A and B. Despite orthopteran background noise, irregular amplitude peaks are evident, starting at 0.06 sec from beginning of the trace. These peaks correspond with the vertical striations of the sonogram.



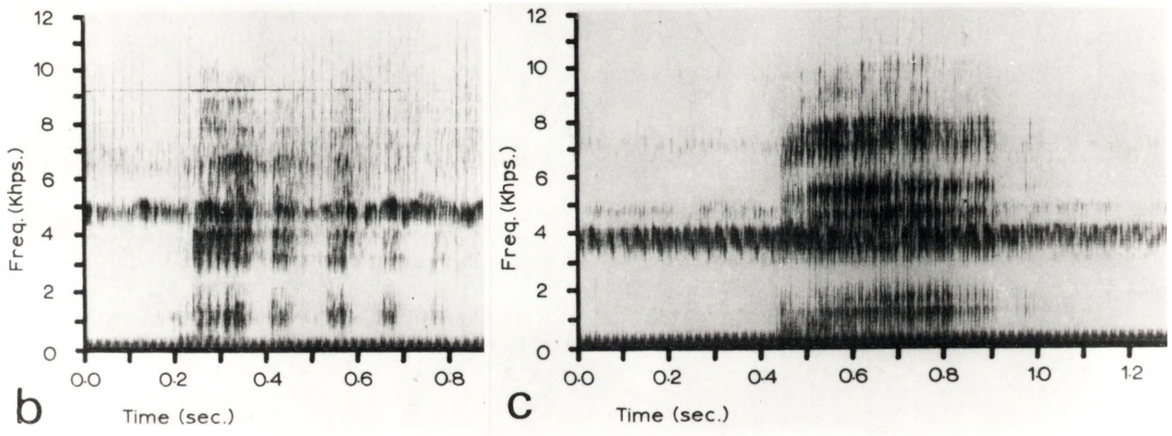


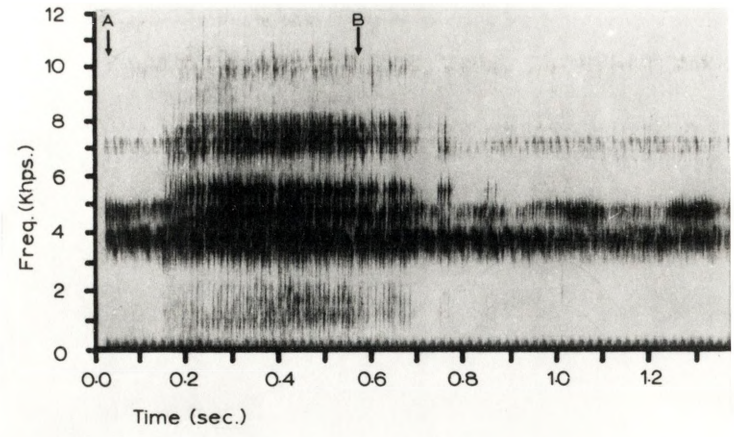
Figure 4.14: a) A chatter phrase with a long initial unit followed by 6 fading shorter units, the last at 1.36 sec.

b) Chatter phrase with a shorter initial unit followed by 4 shorter units.

c) Chatter phrase consisting of a long initial unit followed by one very faint short unit at 0.98 sec.

Note vertical striations particularly in initial units of b and c.

Ignore orthopteran background noise at 5 Kh.



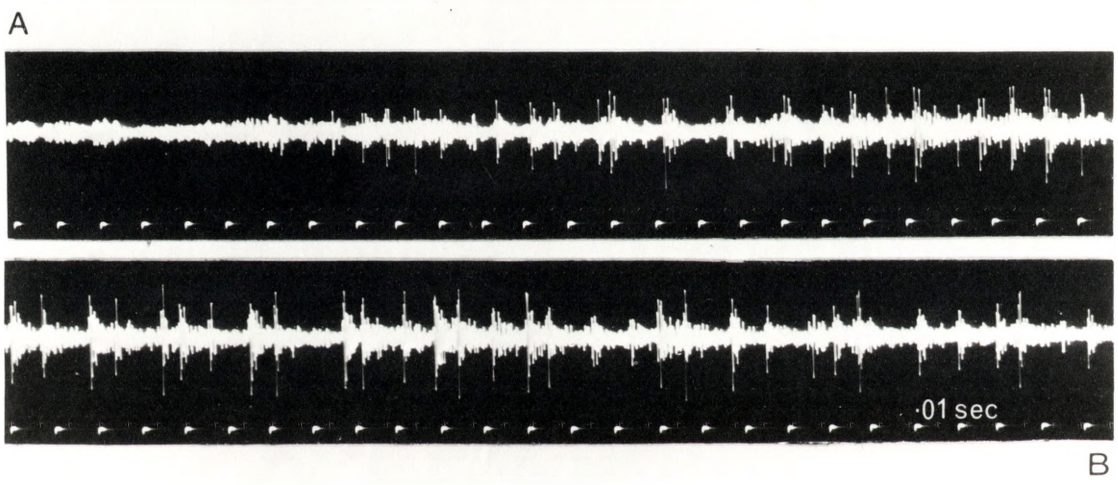


Figure 4.15: Sonogram - three unit chatter phrase (2nd unit at 0.75, 3rd unit at 0.85 sec). Ignore orthopteran background noise 3.5 to 5.0 Kh.

Oscillogram - trace of above sonogram between A and B. Despite orthopteran background noise, irregular amplitude peaks are evident, starting at 0.06 sec from beginning of the trace. These peaks correspond with the vertical striations of the sonogram.

Table 4.1

Length of unit, dependent on its position in a chatter phrase, and length of time interval between the units of a chatter phrase

Unit of Phrase	Interval between Units	No. measured	mean (sec)	Length Range (sec)	S.E.	Coef. of variability %	Standard deviation
1st		14	.351	.07-.54	.041	45.5	.153
	1st	14	.043	.02-.11	.006	49.3	.021
2nd		14	.060	.03-.11	.006	34.2	.021
	2nd	14	.052	.03-.12	.006	43.5	.023
3rd		14	.050	.02-.07	.004	29.6	.015
	3rd	10	.054	.04-.08	.004	21.1	.011
4th		10	.045	.03-.06	.003	20.9	.009
	4th	7	.067	.05-.09	.005	20.0	.013
5th		7	.046	.03-.06	.005	28.3	.013
	5th	3	.073	.07-.08			
6th		3	.037	.02-.07			
	6th	2	.060	.05-.07			
7th		2	.045	.02-.07			

Its rough quality is owing to its amplitude structure which shows as clear vertical striations on a sonogram (Figs. 4.14a, 4.14b, 4.14c, 4.15) and as pronounced peaks, about 120/sec, on an oscillogram (Fig. 4.15). The amplitude structure is very similar to that of the growl and formant positions appear to be the same. The two are distinguished only by the chatter being phrased. Some sonograms of the chatter, particularly Figure 4.14c, show traces below 1.0 Kh, but although very similar to a grunt in this respect the chatter trace does tend to fade markedly at 0.5 Kh. The chatter, therefore, appears to be an extension of the grunt-growl continium.

Characteristically a chatter phrase (e.g. Fig. 4.14a) starts with a loud unit of variable length followed at regular intervals by shorter units of approximately equal length (Table 4.1). The first unit is always the loudest with subsequent units becoming fainter and fainter, making it difficult to determine the number of units per phrase. However, both aural counting of the number of units per phrase direct from a tape recording (no. 78, mean 4.71, S.E.0.147, range 2-8) and sonograms (no. 14, mean 4.6, S.E.0.37) give similar results.

During field observations chatters were divided into two types, depending on whether they continued for more than five minutes, (measured to the nearest half minute). Although five minutes is an arbitrary division it was based on field observations that most chatters lasted two to three minutes, but a few continued for longer and of these most continued for much longer than five minutes.

A long chatter is a bout which lasts for more than five minutes. The lengths of ten long bouts measured were respectively, 7,10,13,15,17, 18,25,25,36 and 45 minutes, showing a continium, but with most considerably longer than five minutes. A 15 min. segment of a 25 min. bout was tape recorded and contained 76 phrases (an average of 5/min.). The time interval between the beginning of successive phrases is fairly constant, but with the occasional longer interval dividing the bout into sub bouts (mean 11.9sec,S.E.1.38,no.75,range 2.25-90.80 sec.).

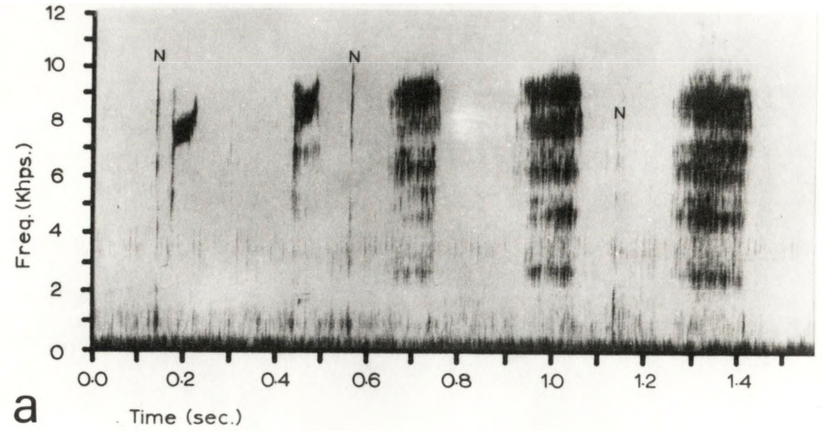
Typically the first few phrases in a bout are loud and guttural. Gradually the phrases become softer until the call almost fades away, but it is then maintained by a renewed burst of energy.

A short chatter is a bout that lasts less than 5 minutes, but which contains at least two phrases (c.f. brief chatter below). One of two bouts, however, did last about 5 minutes so the distinction between the long and short chatters is not entirely clear cut. The number of phrases counted in 11 short chatters made by free ranging possums at Tyne St. varied from 4 to 16 with a mean of 9.2 ± 2.8. Assuming a similar time interval between phrases as in the long chatter the length of these 11 bouts would have ranged from 0.6 to 3.0 minutes. Like the long chatter, the short chatter bouts are often divided into two or three sub-bouts by slightly longer pauses between phrases.

Short chatters start loud and gradually fade away, and typically lack renewed bursts of energy.

The brief chatter was not recognised until extracting data from the field notes, when it became evident that short chatters were often qualified as brief, very short or explosive. In retrospect these qualified short chatters occurred in a particular context, discussed later, and consisted of only one phrase which was usually short or probably even truncated. Although the recognition of this category of chatter has included contextand is therefore not strictly syntactical, I suspect that it will be possible to recognise it structurally and that it may be very similar to a growl.

Minor variations occur either during or between phrases of the long and short chatters. In one case it was possible to identify an individual, Male 6174, by a high pitched piping sound occurring with each phrase. A rudimentary screech terminated a few phrases at the end of a long chatter bout given by Male 33, and in another case the beginnings of a screech was inserted between the second and third unit of each phrase. Juvenile Female 42 gave one or two soft grunts between some phrases of a long chatter.



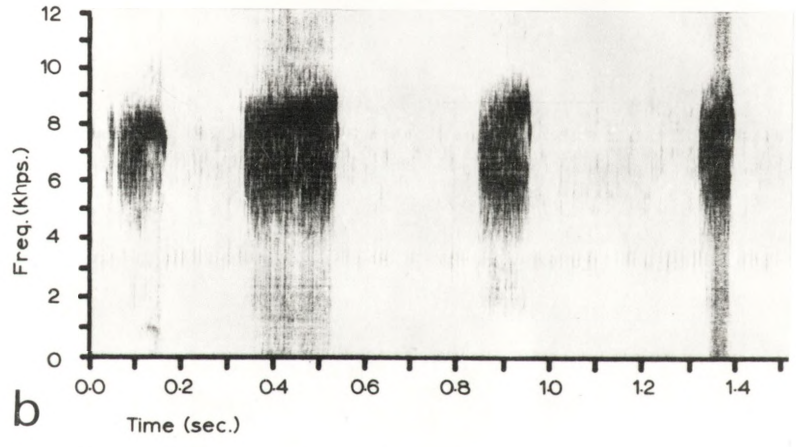


Figure 4.16: Two squeak phrases made by a 51 day old joey when removed from its mother's pouch.
a) First two units at 0.2 and 0.45 sec show definite tonal elements. (N = machine noise.)
b) Tonal elements not as pronounced as in a.

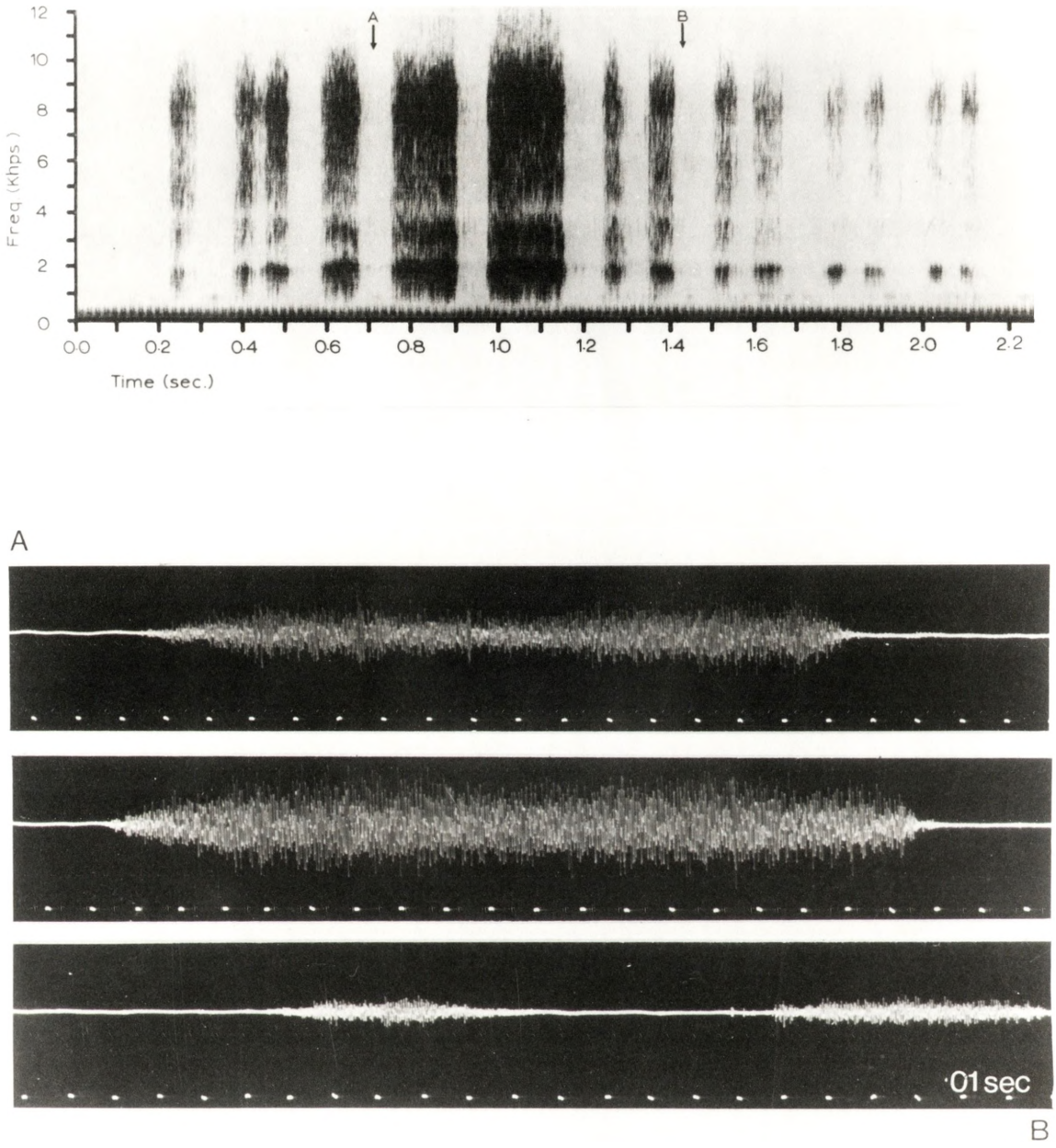
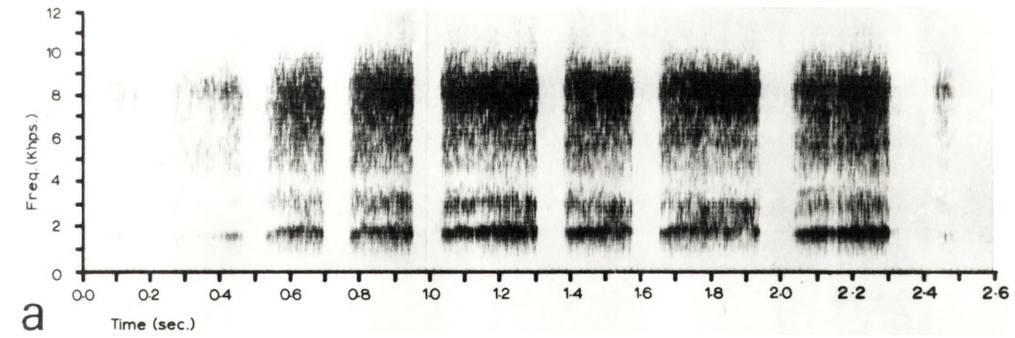


Figure 4.17: Sonogram - a fast zook-zook phrase, made by a 145 day old joey, with 12 short units and two longer units. The short units tend to occur in pairs. Formants at 1.75, 3.0 and 8.0 Kh rising slightly in the middle of the phrase.

Oscillogram - 4 units of the above zook-zook phrase between A and B. Note smooth amplitude pattern.



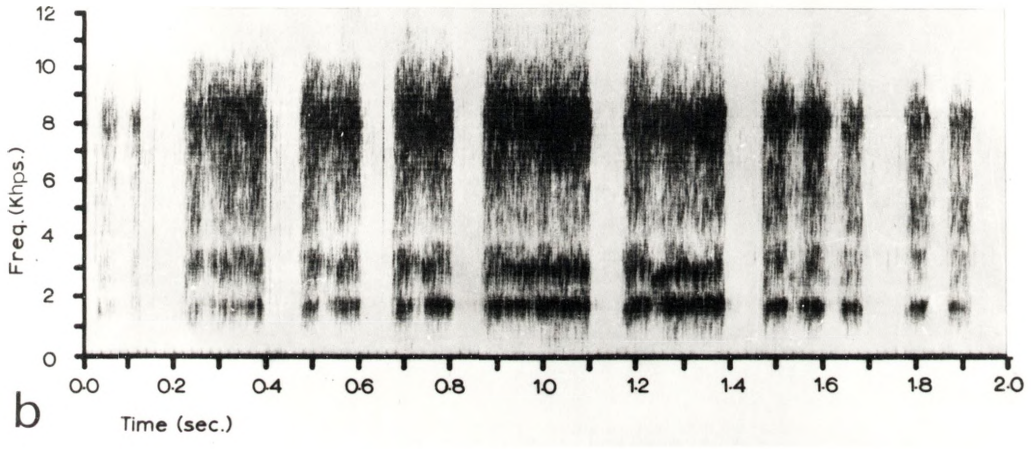
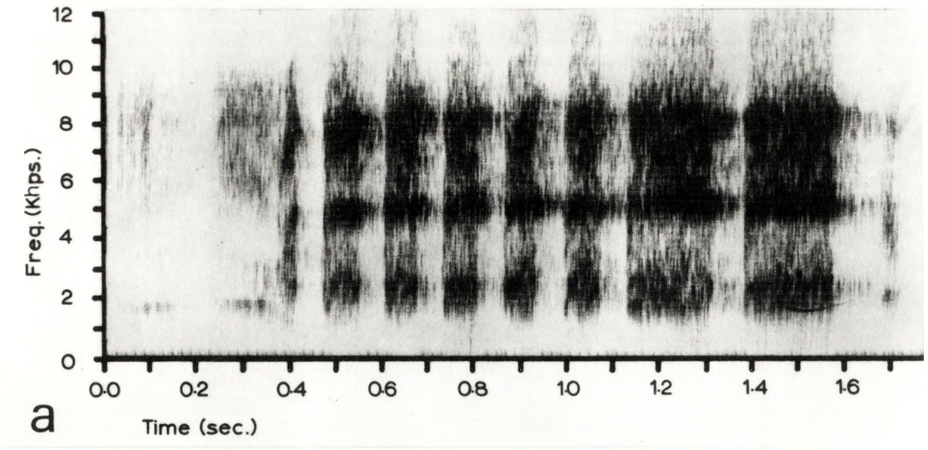


Figure 4.18: a) A slow zook-zook phrase with 9 units, the first (0.1 sec) and last (2.48 sec) being very faint. Formants at 1.75, 3.0 and 8.0 Kh. Age of joey = 145 days.

b) Zook-zook phrase showing transitional stages between the fast and slow variants. The last two units (1.8 and 1.9 sec) are short units. The unit between 1.48 and 1.7 sec has partially separated into three shorter units. The lower formants of the 3rd (0.5 sec) and 4th (0.7 sec) units show a break indicative of a partial separation into sub-units. Age of joey = 145 days.



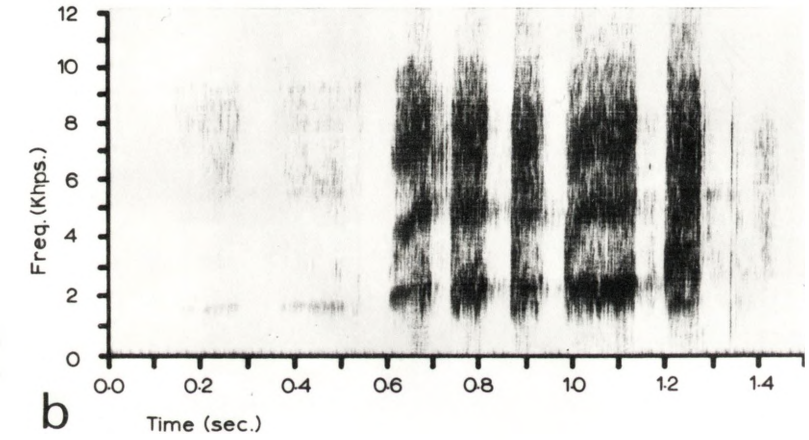


Figure 4.19: a) Zick-zick phrase; formants at 1.75, 5.0 and 8.0 Kh. Note 2 soft zook-zook units at the beginning of the phrase, with a sudden transition into a zick-zick in the 2nd unit. Age of joey = 145 days.

b) Zick-zick phrase, again with two soft zook-zook units at the beginning. Note rise of the middle formant in the 3rd unit (at 0.65 sec) from 4.0 to 5.0 Kh. Age of joey = 145 days.

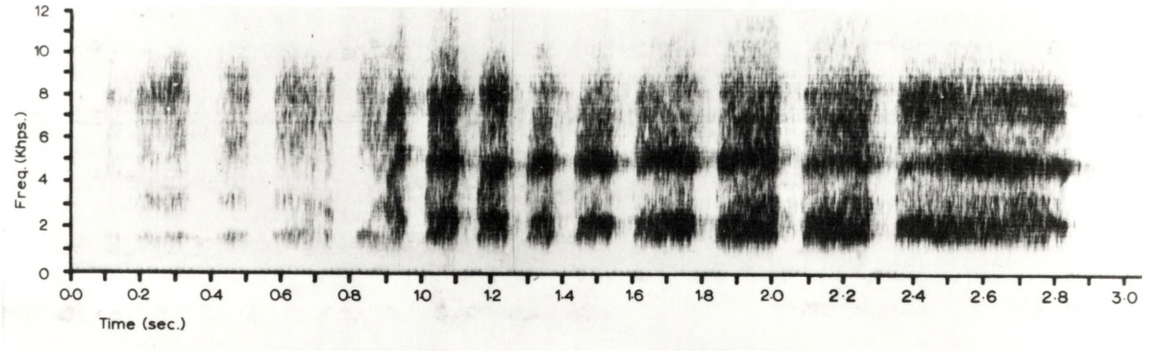


Figure 4.20: A long zick-zick phrase. Note sudden transition from soft zook-zook units to the more intense zick-zick units. Age of joey = 145 days.

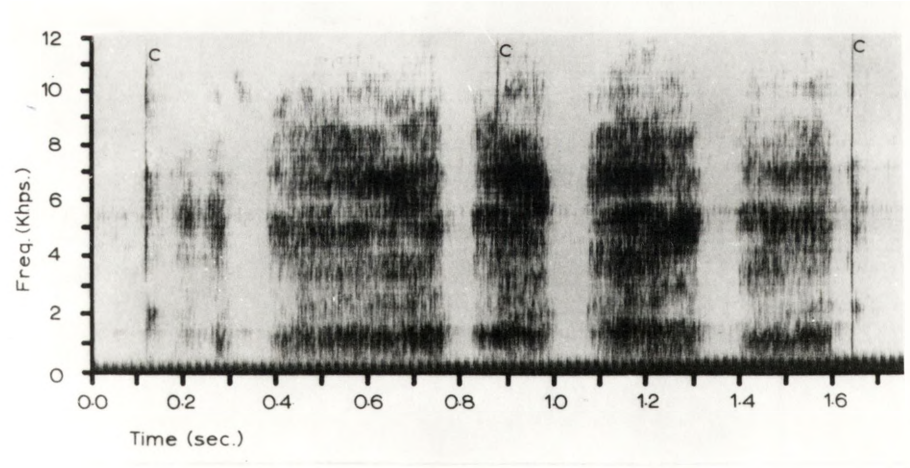


Figure 4.21: A slow shook-shook phrase of 5 units. The first unit (0.2 to 0.3 sec) divided into two sub-units. Formants at 1.5, 5.25 and 7.0 Kh. Three clicks (C) present, made by the same animal.

4.14212 Squeak

The squeak is a high pitched rather weak call and is the only one in the repertoire of the possum which contains tonal units (Fig. 4.16). A strong formant between 7.5 and 9.5 Kh is the only consistant feature in the frequency pattern of the two phrases shown on the sonograms (Fig. 4.16a,b). Its high pitched thin quality makes it difficult to judge the distance over which the call could be heard, but it is in the order of 10m. Only early pouch young gave the call (see also Kean 1967) and it is probably an early stage in the ontogeny of the "zook-zook" call, described next.

4.14213 Zook-zook

The zook-zook call is a rapidly repeated unvoiced zook-zook-zook-zook

Two variations with clear transitional stages are recognised. A fast zook-zook (Fig. 4.17) with shorter units (range 0.04-0.14sec) and the same three formants. Secondly a slow zook-zook (Fig. 4.18a) with comparatively long units (range 0.10-0.49sec) and three clear formants (1.75,3.0,8.0 Kh) the highest of which is the strongest. In both the fast and slow zook-zook the formants gradually rise by 0.5 Kh to the middle of the phrase then gradually fall back to their original position.

Short units of the fast zook-zook tend to occur in pairs (Fig. 4.17), which may partly join (see 2nd & 3rd unit at 0.4 of 4.17) or coalesce more fully to form single units (Fig. 4.18b), thus forming a transitional series between the two variations.

Amplitude structure of the zook-zook is smooth. (Fig. 4.17)

4.14214 Zick-zick

The zick-zick call is a rapid intense zick-zick-zick which was not distinguished in the field from the zook-zook. The distinguishing features are that the zick-zick is much more intense, and the middle formant is at 5.0 Kh (Fig 4.19) instead of at 3.0 Kh. (Table 4.3). In all examples (Figs 4.19a,4.19b,4.20) the zick-zick phrase starts with two to three zook-zook units, then rapidly changes to the zick-zick either in the middle of a unit (Fig 4.19a) or from one unit to the next

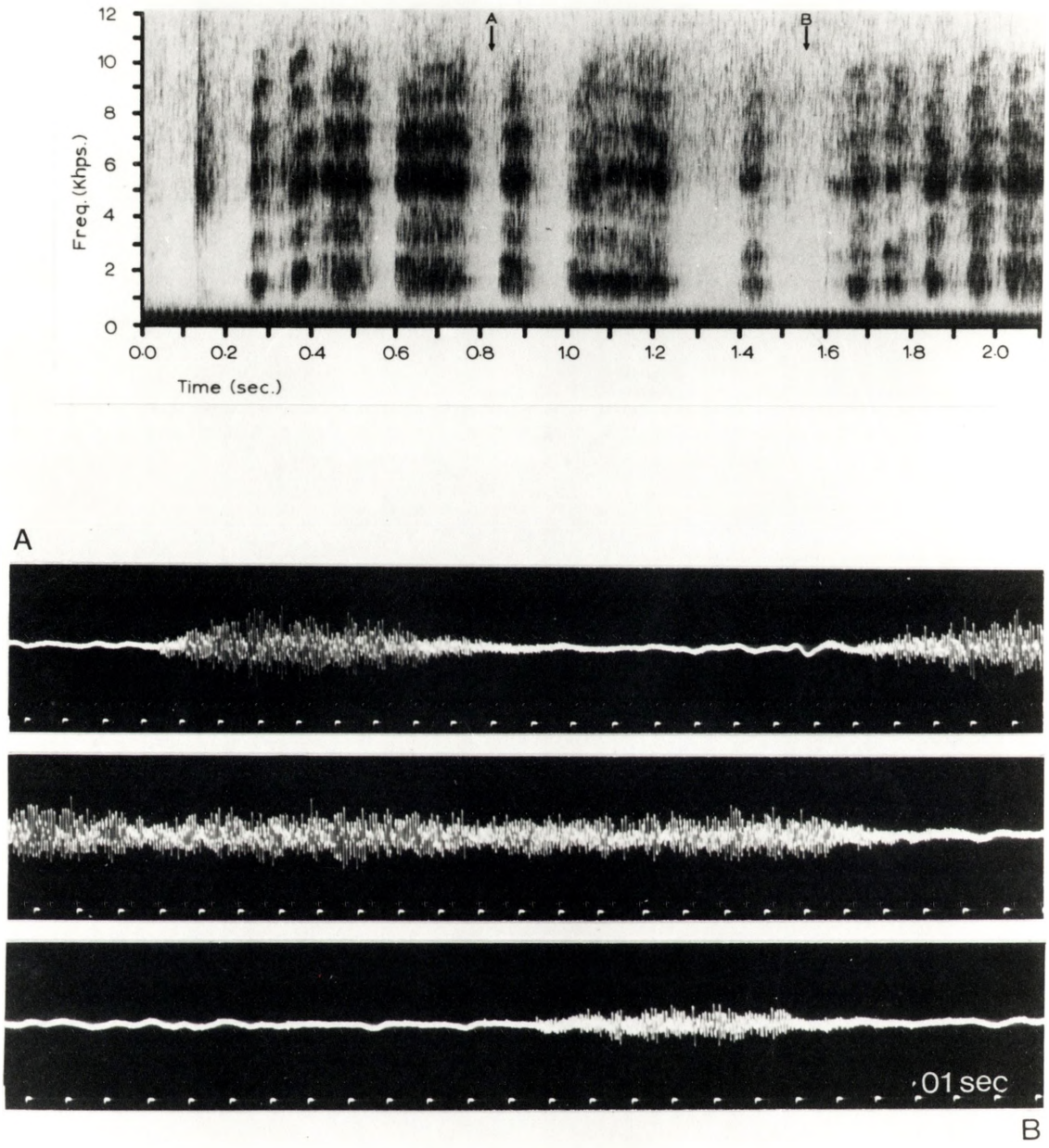
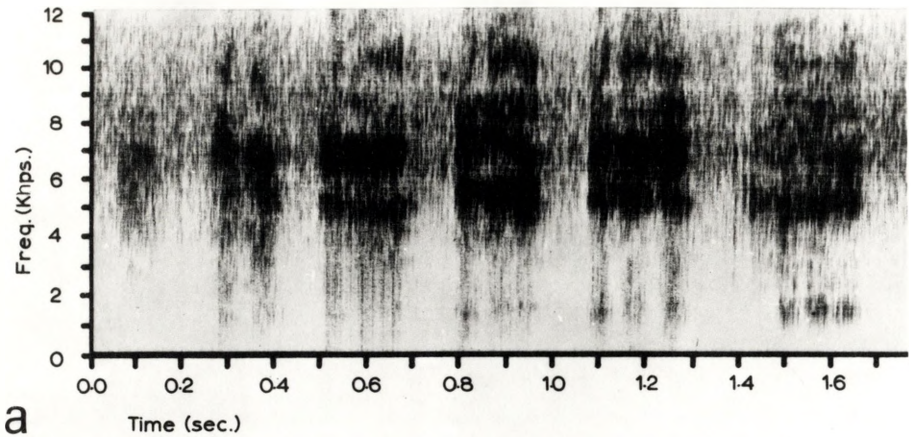


Figure 4.22: Sonogram - a fast shook-shook phrase. Note the comparatively large number of short units, some of which are partly coalesced. The unit at 0.15 sec is probably a click.

Oscillogram - two short and one long unit of the above sonogram between A and B. Note smooth amplitude pattern.



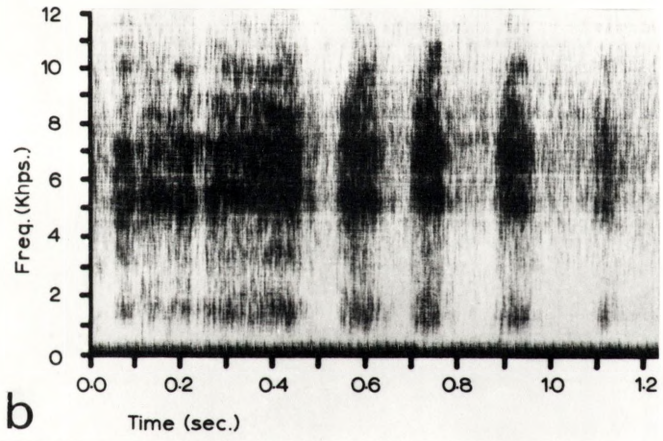


Figure 4.23: a) Shook-shook phrase in which some units (e.g. at 1.2 and 1.3 sec) show clear subdivisions. These are transitional between the long units of the slow variant and the short units of the fast variant.

b) Shook-shook phrase showing an abrupt change from long to short units.

Table 4.3

Structural classification of sounds given by Trichosurus vulpecula. Solid arrows connect sounds closely related structurally. Broken arrows connect sounds which fuse to form complex sounds. Ontogenetical relationships are indicated by one way arrows. : = exclusively juvenile, + = exclusively male. (Sounds not included - wheeze, sneeze, snuffle, gag).

Frequency Range Kh	Amplitude Pattern	Sound		Sound Source
		Non-phrased	Phrased	
<12	Rough	(Cough?) ↕ Grunt ⟷ Growl ⟷ Brief Chatter ⟷ Short Chatter ⟷ Long Chatter		Larynx
	Smooth	Hiss ⟷ Screech	Zick-zick: ↕ Squeak: → Zock-zock (fast, slow) → Shock-shock+ (fast, slow)	
>12	Pulse	Click (regularly spaced but not phrased)		Buccal Cavity

(Fig. 4.19b). In all three sonograms, but particularly Figure 4.19b, the first intense unit of the phrase shows a sharp rise in the position of the middle formant from about 4.0 to 5.0 Kh. This suggests that the middle formants of the two variants are homologous.

Table 4.2

Position of major formants (Kh) of smooth amplitude phrased calls.

Squeak	- between 7.5 & 9.5
Zook-zook	- 1.5, 3.0, 8.0
Zick-zick	- 2.0, 5.0, 8.0
Shook-shook	- 1.5, 5.0, 7.0

When considering the zook-zook and zick-zick calls as one, which was done in the field, the carrying capacity ranged from about 2m to over 80m depending on the intensity of the call. Presumably the higher pitched more intense zick-zick is the call that carries furthest.

4.14215 Shook-shook

The shook-shook call is a soft rapidly repeated unvoiced shook-shook-shook-shook, with a maximum carrying capacity of about 20m. It is distinguished from the similar sounding zock-zook mainly by its lower pitch and on sonograms by the different distribution of the major formants (fig. 4.21) (see also Fib. 4.10) which occur at 1.5, 5.25 and 7.0 Kh (Table 4.3).

Two variations occur which are similar to those of the zook-zook. In the slow shook-shook (Fig. 4.21) units are longer (0.15-0.35 sec) than in the fast shook-shook which has a basic unit length of about 0.05 sec (Fig. 4.22). The shorter units of the fast call may be quite distinct, partially joined (Fig. 4.22), or almost completely joined (Fig. 4.23a) to give a transitional series from one variation to the other.

A distinct 'free-wheeling' repetitive quality is imparted to the fast call by the rapidly occurring short units, which easily distinguishes the fast call from the slow. Abrupt changes from the slow to fast variation may occur in the middle of a phrase (Fig. 4.23b).

Amplitude structure of the shook-shook is smooth. (Fig. 4.22).

4.143 Miscellaneous sounds

Both coughing and sneezing were heard, but no effort is made to describe these further, except to say that a cough was sometimes recorded in the field notes as a coughing grunt.

Snuffling sounds can sometimes be heard when a possum is within about 50 cm and these seem to be associated with sniffing.

Faint wheezing presumably caused by laboured breathing, was once heard after Victor had exerted himself by following Cleo round their cage.

Kean (1967) refers to the sound of lip smacking, which he claimed attracted other possums to food. I never heard this sound. It may be a variation of clicking, but Kean also mentions clicking as a distinct sound.

Ridpath (1967 p.54) describes what she calls "a kind of tooth-rattling" performed by males, and involving a slow movement of the jaw. I never heard this unless she is referring to clicking.

Gagging was sometimes heard when a possum was retching (see Appendix II).

4.144 Syntactical affinities of sounds

A structural classification of the sounds which have been analysed in details is presented in Table 4.3. Sounds such as the cough, wheeze, sniffle, sneeze and gag have not been included in the classification because they were not recorded on tape.

Three attributes are used to construct the classification. Firstly the total frequency range which separates the click from the other sounds by the click's narrow but clear trace right on the top of the sonogram and probably well beyond 12.0 Kh. This may be owing to the click originating in the buccal cavity whereas the other sounds are vocalisations originating in the larynx. Secondly, amplitude pattern which again isolates the click because of its rapidly fading single pulse, but which also divides vocalisations into two distinct groups. One group has pronounced intra-unit amplitude peaks, possibly produced by the rather flaccid vibration of the epiglottis, and includes the grunt, growl and chatter. The other group lacks these pronounced peaks and is a fricative sound, possibly produced by air passing between the large arytenoid cartilages and not by the vibration of vocal folds which the possum

lacks (Negus 1929). Thirdly phrasing divides groups based on amplitude pattern into nonphrased and phrased sounds, but the clarity of demarcation is different for the two groups. In the peaked-amplitude group there are transitional stages between a non-phrased growl and a phrased chatter, whereas in the other group, although transitional stages were observed between the hiss and screech, the phrased and non-phrased calls of the group are distinct. Moreover, both the zook-zook and the shook-shook are significantly less variable than a chatter in the number of units per phrase, indicating that they are more stereotyped calls (Table 4.4).

Table 4.4

Number of units/phrase in phrased calls of T.vulpecula:- measurements from sonograms.

Call	No. of units/phrase				
	No. Measured	Range	Mean	S.E.	coef. of var. %
Zook-zook	6	8-13	10.3	0.76	7.4
Shook-shook	7	5-7	5.8	0.82	14.1
Chatter	14	3-7	4.6	0.12	30.6

Finally, although frequency structure, i.e. formant positions, shows clear differences between some calls, no general frequency groups were detected because variability of the small sample was too great. The clearest separation on frequency structure occurs within the smooth-amplitude phrased group as pointed out in the description of these calls.

Thus three major groups of vocalisations are distinguished. One is the grunt-growl-chatter group which is a graded series in the sense discussed by Marler (1965). It has little apparent difference in frequency structure apart from the low formant of the grunt, but even this may be graded as some chatters show a trace below 1.0 Kh. Basically the series consists of a bipartite temporal change, first in the number of units from the single unit grunt to a chatter phrase with a mean of 4.6 units per phrase, and secondly in the number of phrases (greater than 78) of the longest long-chatter. A second major group contains the hiss and the screech forming another graded series, but in this case based mainly on intensity, length of unit, and an apparently

variable frequency structure. Modification of the two graded series is increased further by the formation of both intra- and inter-group complex calls. The third major group consists of calls which are of the discrete rather than the graded type (Marler 1965). Although the zook-zook grades into the zick-zick the transition is rapid with no intermediate calls occurring which makes them discrete though usually joined calls. No intermediates were detected between the zook-zook and the shook-shook. However this may be owing to the zook-zook being a predominantly juvenile call whereas the shook-shook is an adult call. Twice adults gave a zook-zook but neither were tape recorded. Both the zook-zook and shook-shook have variations, fast and slow, which represent the end points of a limited graded series with clear intermediates. So although they are discrete from each other both are in themselves graded. The relationship between the squeak and zook-zook is purely an ontogenetical one as the squeak is only given by early pouch young.

Size of an animal's sound repertoire is difficult to establish, particularly when graded series of vocalisations are involved. For the possum a maximum of 24 sounds is recognished either as discrete sounds or as modes in a continuum (Table 4.5).

Table 4.5

Maximum repertoire, including all variations, of sounds made by T.vulpecula and recognised either audibly or spectrographically.

1.	Grunt	13.	Slow shook-shook
2.	Growl	14.	Fast shook-shook
3.	Brief-chatter	15.	Slow zook-zook
4.	Short-chatter	+16.	Fast zook-zook
5.	Long-chatter	+17.	Zick-zick
6.	Hiss	+18.	Squeak
7.	Screech	19.	Click
8.	Grunt-screech	20.	Wheeze
9.	Growl-screech	21.	Cough
10.	Hiss-screech	22.	Sneeze
11.	Screech-hiss	23.	Snuffle
12.	Grunt-screech-hiss	24.	Gag

\+ Exclusively juvenile

Although this exceeds the described repertoires of many primates (Marler 1965) comparisons are not usually justified, because the size of the repertoire depends so much on the duration of the study and under what conditions it was done, and also on an authors interpretation of what constitutes a distinct

sound. Possibly the closest comparable study to the present one is that of Struhsaker's (1967) on the vervet monkey in which he recognised 36 distinct sounds.

4.15 Functional Analysis

4.151 Introduction

In this section an attempt is made to determine the meaning of a call. There are two categories of meaning; A in which a sound produced by the possum indicates some underlying motivational or purely physiological state of the animal and can be said to signify this state e.g. an aggressive tendency, tension etc.; and B in which the meaning is determined from the effect it has on other animals particularly conspecifics, e.g. threat, an alarm call etc. The first category Smith (1965) considers to be the semantic meaning of a call, since it signifies a certain state or action. Marler (1965) on the other hand doubts whether it is possible to attribute semantic meanings to signals used in non-human communication, because the observer is a non-participant. Be that as it may, the first category is mainly concerned with study of casual factors. The second category considers the pragmatic meaning of a call, which in the study of social interactions is of more immediate importance. Therefore in this section emphasis will be placed on the determination of the pragmatic meaning of a call (B above) - hereafter referred to as its function, and only occasional reference made to possibly casual factors and a call's signification (A above).

The social function of a call ultimately depends on the response of con-specifics to the call. To a non-participating observer only those responses which show some outward manifestation can be measured. Thus if no response is apparent this does not necessarily mean that the call has no social function, although this possibility has to be considered particularly in a solitary animal. Useful indications as to a call's function can also be obtained from the context in which it occurs, but context alone can never provide more than indications, sometimes very strong indications, of function. However, since it is much easier to collect data on contexts than on responses, the contextual approach is a useful one in a field study of behaviour. Context

can also provide clues of casual factors, and in a field study such as this one is usually the only evidence on which casual relationships are based.

Thus for each call in this study the more numerous contextual data are presented, followed by the response data, and function is determined from a consideration of both. In a few calls where neither contextual or response data give clear indication of function, casual analysis is attempted in the hope that it will clarify an otherwise obscure picture.

Since data for both functional and structural analysis of calls were collected concurrently, more calls were recognised at the end of the study than at the beginning. Thus in the functional analysis some lumping of calls is inevitable.

For the functional analysis the only observations used are those in which the possum making the sound could be seen and hence the context known. However, in contexts which involved two or more possums it was often impossible to determine which possum gave the calls, even though they all could be seen. These observations are included, but a distinction is made in the text between these and the observations in which it was possible to determine the calling possum.

4.152 Screech

A screech includes all variations of the screech including the complex forms, and it also includes hisses. Only occasional references are made to the various types included in this category.

4.1521 Context

(i) Face-to-face (89 obs.). Two possums meet face-to-face, and one gives a screech usually when they are within 1m of each other (Table 4.6). Most observations (72) involved a male and female and where it was possible to determine which possum gave the screech (46 obs.) it was always the female. Typically the male approached along a branch. The female would at first give a hiss rising in intensity to a screech if he continued to approach, or which died away if he either stopped or turned back before coming within about 0.5m. A grunt-screech (often recorded as a K-screech) was given if the male approached suddenly, for

example by jumping onto the branch next to the female, or when the female appeared startled by the male's approach.

Table 4.6

Distance in metres in a face-to-face encounter between two possums, when one gave a screech.

Distance (m)	0.5	1.0	1.5	2.0	2.5	Total
No. of Observations	44	9	2	1	3	59

The screech in this context is not exclusively a female call because it did occur in one male-male interaction. Similarly it is not exclusively adult because juveniles also gave screeches (5 obs.).

Other behaviour such as a raised front paw or an occasional bipedal threat were sometimes associated with the screech.

(ii) Rear-approach (11 obs.) is very similar to the previous context except that the approaching possum comes up to the other from behind. Again most observations (9) were male-female interactions in which the male approached the female, and when within 0.5m she spun round to face him, at the same time giving a loud screech without a preliminary hiss. It tended to be a K-screech accompanied by a raised front paw.

(iii) Lunge (9 obs.) All interactions were male-female in which the female lunged forward at the male. A screech occurred at the same time and in eight it was definitely given by the female.

(iv) Chase (14 obs.) Sometimes during a chase a screech usually accompanied by a grunt was given. The screech and grunt usually occurred at the beginning of the chase, so effectively the context is similar to the lunge. However, in at least two observations it was the chased possum, both times a male chased by a female, who gave the screech and grunt.

(v) A fight was often accompanied by screeches (36 obs.). When the fight was a brief scuffle the screech was short and sometimes associated with a grunt, but in prolonged fights the screech was often loud

and long and frequently punctuated by growls and grunts. It was difficult to determine which possum gave the screech, but in several observations it seemed to be both.

Twice during a fight the screech took on a distinct quality which seemed indicative of pain. For example when Donald was biting and pulling at Male 6181 who was mounted on Lesley, Male 6181 suddenly gave a sharp comparatively high pitched screech, almost a squeal, and hurriedly dismounted.

(vi) During mating when the male was actually mounted on the female, vocalisations varying from a quiet hiss to a very high intensity screechwere sometimes given (6 obs.). In three of these the screech was definitely made by the female as she tried to dislodge the male, and in the others they were probably given by her.

(vii) During handling screeches were sometimes given, particularly by adult males. The male usually lay back in the trap or sack with his mouth wide open and one paw raised ready to strike as he hissed. The intensity of the hiss sometimes rose to a screech. One six month juvenile when picked up by the tail gave quiet screeches and a few soft grunts.

4.1522 Response

Two categories of response were observed; one in which a possum participated in the interaction which produced the screech, responded to the screech; the other in which a non-participating possum responded to a screech.

In the first category one has to be careful that the possum is responding to the screech and not to some other cue such as a raised paw, or the other possum moving towards it. Hence the only context which can be used to determine this is the face-to-face, and then only the observations in which the screech was not accompanied by a raised paw or a bipedal threat. Although a screech involves opening the mouth, which in itself may act as a visual cue, the open mouth is not considered an important cue to a nocturnal mammal.

The most obvious response is for a possum to suddenly jerk back when the other possum gives a screech, particularly if the screech was a short

sharp screech without a preliminary hiss. The most common response was for the approaching possum i.e. usually the male, to move away either by turning round and walking back down the branch or occasionally by jumping to one side. Another response of the same type was for the approaching possum to stop. (Table 4.7).

Table 4.7

Responses given by a possum to a screech made by another possum. Only contexts in which a screech alone occurred, without other overt behaviours such as paw raising, are included.

Context	Response	No.		Result
Face-to-face	Stopped	7	33	Caused withdrawal
	Moved away	20		
	Jerked back	6		
	Continued to approach	7	9	Neutral
	Continued to enter den	2		
Juvenile meets Strange adult	Mother ran to juvenile	6		Attracted mother (caused withdrawal of strange adult)
Distant screech	Turned towards screech	3		Attracted attention of distant possum

Although some sort of withdrawal response was the usual one to a screech in a face-to-face context there are exceptions. Sometimes a male continued to approach a female apparently ignoring her screeches and, for that matter, other postures such as a raised paw. In all of these observations except one, the female was close to being ready to mate. In the exception a male appeared preoccupied with sniffing the branch as he ran along it towards a female, and he appeared unaware of the female who jumped to one side when he was less than a metre from her. The other situation in which a possum continued to approach another which was hissing or screeching was when a juvenile entered its mother's den at dawn, after she had entered. Hisses of various intensities came from the den, presumably made by the mother. Although the juvenile hesitated at the entrance it then entered the den rather more slowly than if the den had been empty.

In other contexts where the screech was accompanied by some other

behaviour, the general response was similar to that found in the face-to-face context i.e. usually one of withdrawal.

The second category of responses was one in which a possum responded to a screech, without being involved in the interaction producing the screech. Although a possum usually apparently completely ignores a screech given during an interaction between two other possums, even if as close as 10m, there were times when the non-participating possum definitely responded to a distant screech.

A female's response to a screech given by her dependent juvenile was the most marked response of this nature. A juvenile screeched whenever it met a strange possum - adult males in all cases - and the mother who was usually in the same or adjacent tree, immediately climbed rapidly to join her young one. The female's approach was usually sufficient to make the male withdraw. There was little doubt that the female could distinguish a juvenile screech from an adult screech, and from it recognise that her juvenile was in a situation which needed her help. Individual recognition is not necessarily implied because in all observations only one juvenile and one female were in the vicinity. In one of the observations a male as well as the juvenile's mother responded to the juvenile's screech. Male 20 had pinned Hester's juvenile to the ground and its screech brought both Hester and Donald rushing over to it, and it was Donald who actually attacked and drove off Male 20.

Responses to distant screeches were also shown by males on 3 occasions. In one Male 22 looked up from chinning a stump, in the direction of a screech. In another Donald leapt onto the base of a tree, apparently in alarm in response to a nearby screech and looked in its direction. In the third observation Victor, who was trotting about on the ground apparently looking for something, suddenly changed direction and headed towards a tree containing Male 33 and Female 22, when one of them gave a screech. Victor then climbed the tree to join them.

4.1523 Function

The screech occurs only in agonistic interactions and is frequently associated with behaviour which is indicative of aggression e.g. raised front

paw, bipedal threat, lunge, fight. Thus by association the screech would appear to be an aggressive behaviour, and since it often occurs in interactions in which no bodily contact is made it can be considered an intention behaviour of aggression, in other words threat. In some chases it was the possum being chased who screeched, but even in this a function of defensive threat (Ewer 1968) is more likely than any function of submission.

Since the most common response to a screech is some form of withdrawal (Table 4.7), the screech is functioning as a threat, which can be defined as any behaviour which "....does not wound, but tends to prevent the approach or cause the withdrawal of a member of the same species." (Barnett 1967 p98). Where a possum continues to approach, the threat of the screech is apparently overcome by a stronger stimulus causing approach, such as a female ready to mate or a home den. The conflict between the two tendencies to withdraw and approach is illustrated by a juvenile's more cautious entry into a den when its mother is already in the den and hissing.

Fights in which screeching is a prominent feature appear to be less vigorous and less likely to cause injury than in prolonged silent fights. Screeching takes the place of biting in the noisy fights, and is an aggressive element in these fights, but one of threat rather than actual fighting.

Although the immediate function of a screech is threat, it may take on other functions to possums not actually involved in the interaction. This is the case of the juvenile screech to which the female responds by rapidly approaching the juvenile. The juvenile is threatening the strange adult, but effectively its most important function is that its screech conveys information to its mother. She appears to recognise that her juvenile needs help and reacts accordingly. Therefore in this context the screech is functioning as a distress call of a particular kind.

Similarly an adult male may recognise the context of a distant screech and if motivated to do so, as in the case of Victor, he will approach the source.

A hiss or screech apparently expresses a readiness to fight, or in other words they signify an aggressive tendency, the strength of this tendency

being positively correlated with the intensity of the call.

4.153 Grunt

Grunts are divided into those which are closely associated with screeches either as complex calls, or as separate calls but in the same context, and those which occur alone.

4.1531 Context

Grunts were frequently closely associated with screeches during face-to-face interactions (13 obs.), chases (5 obs.), and fights (15 obs). In five male-female fact-to-face interactions in which it was possible to tell which possum gave the calls, it was the female who gave both the screech and the grunt. On the other hand, in some fights probably both the male and the female grunted and screeched.

Grunts alone (34 obs) were given in several contexts.

(i) Face-to-face (5 obs) In three a male and female met and it was the female who grunted, in one the male responded by jumping to the ground, but in the other two the female grunted as she turned away from the male. In the fourth observation a male suddenly met a juvenile, just after he had lost a fight with its mother. He grunted, as though surprised, and immediately turned and ran back down the branch. In the fifth observation a mother and her dependent juvenile met nose-to-nose and one grunted just before the juvenile climbed onto its mother's back.

(ii) Chase (12 obs) When a grunt alone was given it tended to occur towards the end of the chase, whereas when associated with a screech it tended to be near the beginning. Some grunts were soft, others loud, some single, while others were given as a rapid staccato series of two to three. Only once was it possible to detect which possum gave the grunt. Female 37 was hanging head down on the trunk of a tree, looking at her juvenile 2-3m below her and hissing. She then chased it down the trunk for about 7m giving several loud grunts as she did so.

(iii) Fight (8 obs) When a grunt alone was given it was usually a single grunt (6 obs), which tended to be given during the more vigorous screechless fights, but in one, two grunts were given. In the last

observation several grunts were given, probably by the male, as he pulled away from a female who was biting at his hindquarters.

(iv) Give-way (7 obs) A possum sometimes grunted as it gave way to another possum (3 obs) or as it bounded up a tree away from another species such as a cat or myself. (3 obs). For example, the young Female 19 gave a grunt as she bounded up a tree ahead of Eve, who jumped onto the base of the tree but apparently took no notice of the younger animal. In another example Female 23 gave several staccato grunts as she climbed a tree when apparently startled by my approach.

(v) Miscellaneous A long series of grunts, many of which were almost screeches, was given by a female as she moved down a tree ahead of her dependent juvenile. I first saw them just after a subdued hiss. The mother was sitting about 10cm below her juvenile, but after a sudden grunt she began to move down the tree with the young one following about 70cm behind. About 3m further down the trunk the female stopped in a crotch and looked back at her offspring for the first time. She continued to give screech-like grunts, and the juvenile stopped 50cm above her. After looking in my direction briefly she gave another screech-like grunt while facing the younger possum. Soon after this they continued down the trunk as before except that there were no further calls.

I was able to provoke grunts from cornered captive possums, males in particular, by a sudden movement of the hand towards them while close to them. The males were usually in a threat posture with mouth open and one or both paws raised. Their reaction to the sudden movement was to jerk back, at the same time giving a grunt.

Finally one grunt was given when a male was vigorously pelvic thrusting while mounted on a female.

4.1532 Response

Only two responses were observed which could be attributed to a grunt. In one a fight came to an abrupt end, by the male jumping back when the female gave an explosive grunt. In the other a male and female met face-to-face

on the trunk of a tree about 1m off the ground, she gave a grunt and he jumped down to the ground.

4.1533 Function

Close association of the grunt with the screech suggests a similar function, namely, threat. Particularly as a grunt may fuse with a screech to give a grunt-screech. Both observed responses to a grunt were withdrawal, thus supporting the contention that the grunt functions as a threat. Similarly threat is suggested by the observation of Female 37 grunting as she chased her juvenile down a tree.

On the other hand many grunts, particularly when alone, were given by the withdrawing possum in the give-way and some of the face-to-face contexts. These however, were more indicative of defensive or low intensity threat rather than any possible submissive function as demonstrated by the grunts of a cornered male who showed definite threat postures of a raised paw and open mouth, but at the same time retreated as far as possible.

Incipient threat is indicated by the screech-like grunts given by Female 6147 as she moved down a tree ahead of her juvenile. The grunts appeared to be grading into a screech, and her actions as she moved gave the impression that she was about to threaten her juvenile, but some restraint prevented her from doing so.

Apart from the suggestion that the grunt may act as a defensive threat or be a form of incipient threat, there were times when it appeared to have no communicative value. Grunts given during vigorous fights, and the one given during mating may merely represent the sound of a sudden expulsion of breath owing to muscular exertion.

In most observations the grunt seemed to express surprised annoyance, though the element of surprise varied considerably. Conceivably the degree to which a grunt signifies an aggressive tendency is closely tied to the actions of the possum giving the grunt i.e. whether it is in a threatening stance with a front paw raised to strike, or moving away.

4.154 Growl

Growls were easily confused with grunts. For example, the growl-screech

shown in Figure 4.1 was recorded in the field notes as a series of grunts and screeches. Thus only the most distinctive growls were recorded as such in the field.

4.1541 Context

A total of nine growls were noted during field observations. Three were given during fights; one male-female; one female-female; and one when the female at Tyne Street chased her juvenile out of the roof, and bit at her offspring's tail, giving several growls as she did so. Two growls were given during a chase, and the remaining four after a fight.

The four growls given after a fight occur in a context which differs from any observed for the grunts. There was always a delay of a few seconds between the termination of the fight and the growl. For example, after a fight with Alice, Alec ran along a branch and gave a quiet growl three or four times. He then crossed to a slightly higher branch and ran back towards Alice. When immediately above her, he stopped and gave another growl.

4.1542 Response

When a growl was given during a fight or chase it was impossible to attribute any response to it, and when it was given after a fight no response was detected.

4.1543 Function

Little can be said about the function of a growl, except that it was given during agonistic encounters, sometimes by the winner, and sometimes by the loser of the encounter. One context which is different from that for either the screech or the grunt was that in which a growl was given after a fight had terminated, and may be indicative of some definite difference.

In general the growl appears to express annoyance, thus signifying a low level aggressive tendency.

4.155 Chatter

In the functional analysis of the chatter it has been possible to consider the three types - brief, short, and long chatter - separately, unlike the screech in which several variations were lumped together.

4.1551 Context

4.15511 Brief Chatter

A brief chatter was given most commonly either during a chase (5 obs), or immediately after a chase (5 obs) or fight (6 obs).

When given during a chase it was twice possible to tell which possum gave the chatter. In both it was given by a female as she chased another possum, a male in one and her own juvenile in the other. In this second observation Female 37's youngster shot out of their den with its mother chasing it. Female 37 kept her nose level with the base of the other's tail for about 7m and gave a brief guttural chatter. This context was almost identical to the one in which Female 37 grunted as she chased the same young one. It was also similar to the context in which the female at Tyne St. growled as she bit at the base of her juvenile's tail. Thus the grunt, growl and brief chatter are not only very similar in structure, they may also be given in very similar contexts.

Like the growl the brief chatter may be given after an encounter has terminated, in this case either a chase or a fight. When given after a chase both possums had stopped, although they may have still been in the nose to tail position a few metres apart. When given after a fight the context was the same as that described for a growl. Where it was possible to tell which possum gave the chatter it was the chasing possum (2 obs) in the case of a chase. In one of these chases Alec had come out of his den at dawn to chase away the young male, Bill. The chase lasted about 3m and just as Alec was about to re-enter his den he gave a brief chatter. In the other a female chattered as she chased a male. In a fight, on the other hand, it was the possum who moved away (2 obs) who chattered, in both cases a male after a fight with a female.

Isolated instances of brief chatters occurred in other contexts; one after a give-way, another during a fight, a third after an alarm dash onto a tree, and a fourth during a lunging attack. In one other, Male 32 was feeding on the ground a metre from me, when he suddenly sat up in the upright alert position, facing away from me, and gave a short

sharp chatter the beginning of which was almost a grunt.

4.15512 Short Chatter

A short chatter was most commonly given at the end of an alarm dash as the possum was clinging to the trunk 1½ to 5m off the ground (10 obs). When chattering the possum looked down presumably towards the source of disturbance which was not usually detected by me. In one case I was the cause of alarm and the possum looked directly at me as it chattered.

In an observation made at Tyne St. the context was broadly that of an alarm dash, but the chatter which followed was considerably delayed. In it the female had started climbing the grape vine and her dependent juvenile attempted to climb the corner of the house, but after frantically scrabbling at the smooth timber the juvenile fell back to the ground with a thump. The noise apparently startled the female who shot up the vine and into the roof. At the second attempt the juvenile reached the beam immediately below the den entrance where it stopped. Soon afterwards (less than 1 min) the female came back out of the roof and touched noses with her juvenile who then climbed onto her back. It was then that the female gave a loud guttural four phrase chatter.

Another common context was for the chattering possum to be sitting on a low branch, either gazing at the ground (6 obs) or into the distance (2obs). In five of the observations the chattering possum was gazing down at another animal, either another possum (once), a cat (twice), a dog (once) or a group of three geese. In all of these the possum appeared to be chattering at the animal on the ground. Both observations of the possum gazing into the distance as it chattered occurred at the same time, in a context which was similar to the others, in that my presence appeared to trigger the chatters. I had been using the full beam of the spotlight to check the ear tags of female 6147 and her juvenile, who were sitting about 7m apart. Within a minute of swinging the beam away from them and while I was still within 25m of the tree,

the adult female began to chatter. They were both crouched-sitting on a branch and gazing away from me. As her chatter phrases began to subside the younger female began to chatter. Thus they were both chattering and looking away from me, apparently gazing into space. Their chatter bouts were of similar length and intensity with the juvenile's continuing after the female's had ended. Although neither possum looked towards me their chatters coincided with my departure, suggesting a cause and effect connection.

Short chatters were given after encounters, either fights (3 obs) or chases (3 obs), in contexts similar to those for the brief chatter. For example, Donald pulled Jack off Lesley's back and chased him down to the ground. Donald stopped 3m from the ground and chattered while looking down at Jack and Male White-tip, both of whom were at the base of the tree. Both males on the ground made half-hearted attempts to climb back up the tree, but were repeatedly chased down by Donald who was sitting on a low branch. Twice more Donald gave short chatters as he sat looking down at the other males. In another observation in which two males had fallen to the ground whilst fighting, both then climbed neighbouring trees and one gave vigorous chatters, after which they groomed themselves for 10 min. Then the silent male chased the male who had been chattering, and who again vigorously chattered after the encounter. Thus it is the chaser or the chased who may chatter.

The one observation of a chatter occurring at the beginning of a fight was similar to that in which Jack and Male White-tip repeatedly approached Donald and were driven back down the tree. In the fight observation Donald was balanced on top of a netting fence and giving guttural chatters, while Male 6181 was clinging to the fence immediately below him. Male 6181 repeatedly approached and withdrew from Donald. Finally a fight started, but by this time Donald had stopped chattering.

A final context was one in which a male chattered while watching two other possums mate (2 obs). In the first observation a male approached a mating pair through the canopy of the adjacent tree and

when about 6m away he stopped. As he sat watching the pair he gave a low chatter at regular intervals. Finally he jumped down beside them and a fight between the males took place. In the second observation Male White-tip had been pulled off Lesley's back by Male 6181 and had shot up the tree to sit about 1m above Lesley. He gave one or two chatters as he sat looking down at Male 6181 who had mounted Lesley, only to be pulled off by Donald and chased down the tree.

4.15513 Long Chatter

A long chatter was most commonly given by a male after he had mated (8 obs), although only in four cases was the whole context observed. Three of the long chatters in which the whole context was observed occurred on the same night when 4 males - 33, 22, Donald and Victor - all mated with Eve in turn. Male 33 was the first to mate with her and after dismounting, which involved a brief scuffle in which he nearly lost his footing, he sat 75cm from her and facing her and began to chatter. The chatter bout lasted for 36 min and stopped only when Male 22 came up the tree. Soon afterwards Male 22 mated with Eve and began to chatter after dismounting. He was interrupted 1 min later by Donald who chased him down to the ground, but 12 min later and when about 35m from the tree Male 22 began to chatter again and continued to do so for a further 10 min. Although strictly speaking, his long chatter had occurred after the chase with Donald and there was a considerably delay, he had started to chatter after he had dismounted and before the chase. However, the general context was consistent with other long chatters which occurred after mating. Donald mounted Eve but did not chatter, then finally Victor mated with her. She broke loose from Victor and turned on him with a screech which sent him rapidly down the branch. He stopped on the same branch and chattered for 25 min. The fourth observation was similar in that a male dismounted after mating, moved to a branch about 1m below the female and chattered for 13 min. In all 4 observations mating appeared to have been successful. In all 4 the female had behaved aggressively either when the male mounted

or dismounted or both.

In the shortest of the long chatters (7 min) Alec sat at his den entrance in the evening and chattered while gazing in my direction; a context similar to that in which a short chatter was given when looking down at another animal on the ground.

Another long chatter (15 min) occurred in a context which may have been similar to the alarm dash context. A possum began to chatter and a juvenile male was found clinging to a tree trunk 4m off the ground. He was looking straight up the trunk and remained in this posture as he chattered, except near the end he began to climb the tree very slowly while still chattering. He then stopped chattering and began to climb at a normal speed.

The longest chatter of all (45 min) was given by seven months old Female 42. She was hanging head down into a diagonal spout in her den tree and remained motionless in this position for 55 mins. For 45 of these minutes she chattered, at first very softly but then at times quite vigorously. It appeared as though she was chattering at something in the spout. I could not see anything, but a pair of kookaburras were in the den a little below the spout, and the spout the juvenile was looking into may have led into the den. She may therefore, have been chattering at the kookaburras, but it was also at about this time that her mother disappeared, presumably died, and the chatter may have in some way been connected with her mother's disappearence.

4.1552 Response

4.15521 Brief chatter

A response to a brief chatter was observed only once. A female was chasing a male down her den tree and one of them gave a chatter. The female's juvenile, who had been following them, immediately turned and climbed back up the tree. Thus a threat function is suggested.

4.15522 Short chatter

A short chatter elicited the most responses. In the mildest form of response a possum turned to look in the direction of a chatter (11 obs)

often interrupting an activity such as feeding, grooming, or cloacal marking. In one of these Alec climbed 1½m up a tree and gazed in the direction of a chatter which lasted 2-3 min, and then jumped back to the ground after the chatter had stopped.

Three times a possum on the ground appeared to respond to a short chatter by making an alarm dash, once after looking in the direction of the chatter, but twice without first looking. Another time Gus climbed a tree in apparent response to a chatter, but without a preliminary alarm dash. In another observation Lesley was clinging to a trunk and chattering, obviously after an alarm dash, and four other possums all within a radius of about 70m were in similar positions on tree trunks, but not chattering. Either they had all responded to the same disturbance, or the other four had responded to Lesley's chatter by making alarm dashes very soon after hers.

The short chatter was the only call of the possum which elicited a vocal response - always another chatter (8 obs). One possum would begin to chatter and after a few phrases another would begin, and sometimes even a third, to form a chorus. The only time that both callers were observed was in the example, already described, of Female 6147 and her juvenile. In that case the responding possum was close to the first possum, but in other cases the possums were up to 100m apart.

4.15523 Long chatter

No apparent response occurred to the long chatter given by a male after mating. The female apparently ignored the chattering male even though he was usually very close to her. Whilst males might have been attracted to Eve by the long chatter of the previous male, the observations are inconclusive.

4.1553 Function and Causation

The most obvious response was the triggering of an alarm dash by a short chatter. Therefore a short chatter, at least in some contexts, functions as an alarm call. Two other responses to the short chatter are consistent with its function as an alarm call. The interest shown by a possum in the location

of a chatter means that the area of disturbance is located, a function which is advantageous to other possums in the area if the source is a ground predator. Similarly by stimulating other possums to chatter, the chatter generally alerts the possum population to danger in their area.

Other functions, even for the short chatter, are suggested by the contexts of the calls. These are speculative to the extent that no definite responses were observed.

Where a brief or short chatter took place during an encounter such as a chase or fight and where it was the chasing possum or the one who initiated the fight who chattered, threat as a function is indicated. The one response where the juvenile turned back up a tree when a chatter was given during a chase between its mother and a male, supports the suggestion that the chatter may act as a threat. Similarly the chatter of a male watching a mating pair suggests threat, particularly as in one case the chattering male precipitated a fight with the mating male.

On the other hand, it was not always the chasing possum or the one who initiated a fight who chattered. Frequently it was the possum who was being chased or had just been chased, or the one that broke away from a fight. Given in this context the chatter indicates submissive behaviour, except that it usually occurred after the encounter had terminated and there was no evidence that the call inhibited the attack of the other possum. An alternative suggestion is defensive threat.

In the typical after-mating long chatter no obvious response was observed, nor does the context indicate any clear function. The male may or may not face the female while chattering, hence if it is a threat it is not specifically directed at the female. She apparently ignores the chattering male so the chatter neither attracts nor repels the female. Possibly the long chatter functions as a signal to other males in the area that the male has succeeded in mating. Since a male often loses all interest in a female after he has mated with her, the chatter may be a cue for other males to move-in and mate with the female.

Causal factors are also useful in assessing the signal value of a call

and hence its possible function. Two causal trends emerge for the chatter. The first and more common trend is one in which the chattering possum has been involved in a situation producing a high level of tension, and the chatter is given in the post-situation phase as tension is reduced. In the alarm dash for example, the chatter is given after the possum has gained the safety of a tree, not before or during the chase. Similarly with a high proportion of chatters given during interactions, the chatter is given after a chase or fight has actually terminated. Female 6147 and her juvenile chattered after I had finished examining them with the full beam of the spotlight. Long chatters are given after a male has successfully mated. For the male, prolonged body contact with an aggressive female during mating is a situation which probably produced the greatest tension. Hence the length of a chatter may be governed by the degree and duration of tension. This is supported by the observations of mating which took place after a long courtship period and in which there is no aggressive behaviour by the female (see Section on courtship), and in which the male does not give a post-mating chatter. A chatter therefore, occurs at a time when tension has been released and may represent a process of "unwinding", and in the semantic sense (Smith 1965) may mean release of tension.

The second causal trend appears to be one in which strong conflicting motivations occur i.e. ambivalent behaviour. When a mother chatters as she chases her juvenile there may be one tendency to attack, but also a strong restraining influence imposed by the mother-joey bond. Similar ambivalent behaviour was displayed by Female 6147 when she gave screech-like grunts as she descended a tree ahead of a joey. Thus the grunt, growl, chatter series may be closely related in causation as well as in structure. A chattering male watching a mating pair shows definite signs of ambivalent behaviour of approach and withdrawal, but not actually approaching while chattering but at the same time showing a keen interest in the others and once by actually initiating an encounter. A male chattering at another male in apparent threat may also be subject to conflicting tendencies of approach and withdrawal because of relatively even matching of the contestants.

Table 4.8

Contextual and functional comparisons of chatters, growls, grunts, and screeches. Contexts are compared on a presence or absence criterion. Functions are considered to be the main one for the call.

Context	Call					
	Grunt	Screech	Growl	Brief chatter	Short chatter	Long chatter
Rear-approach		x				
During give-way	x					
During alarm-dash	x					
During face-to-face	x	x				
During mating	x	x				
During lunge	x	x		x		
During fight	x	x	x	x	x	
During chase		x	x	x		
After fight			x	x	x	
After give-way				x	x	
After chase				x	x	
After alarm-dash				x	x	x
After mating					x	x
Sitting in tree					x	x
Watching					x	

Function	Defensive or Startled Threat	Offensive Threat	Ambivalent or restrained threat			
					Alarm	?

The chatter remains somewhat of an enigma. Functionally there is good evidence that the short chatter is an alarm call, contextual evidence suggests that it may also be used as a threat. This may represent different meanings, at the pragmatic level, of the same call owing to the context. In the context of an encounter or a situation which involves direct confrontation with another animal the chatter may indicate threat. So a possum which chatters after an alarm dash may be threatening the source of disturbance. Similarly a chatter given during or after an encounter may be given as a threat display directed at the other participant in the encounter. Threat in both these cases is probably of the defensive type (Ewer 1968). To a possum who does not actually take part in the situation causing the chatter, and who may be some distance away, the chatter may indicate that a certain type of situation has occurred. If a proportion of these situations are dangerous to the possum i.e. involve a predator, then the chatter will become a danger signal i.e. an alarm call.

Similarly there appears to be a dichotomy of causal factors, with one owing to the release of tension and the other to ambivalent behaviour. If however the release of tension represents the waning of one motivational tendency e.g. fear, then the chatter may be given at a stage where another tendency e.g. aggressiveness, may be in balance with the first overwhelming tendency, i.e. to give a state of ambivalence.

4.156 Contextual and functional comparisons of Screeches, Grunts, Growls and Chatters

These calls considered so far - screeches, grunts, growls and chatters - show considerable overlap both in their contexts and function. There is however, a definite continuum in which the calls at either end show very little, if any, overlap with each other, but are connected by a series of overlapping intermediates.

This continuum is best illustrated by the contexts in which the screech and grunt do not overlap at all with the long chatter, but every other call does to a greater or lesser extent (Table 4.8). Within the continuum there are three main groupings, according to context. In one the screech and grunt form a group, the characteristic feature of which is that the calls occur either

at the beginning of, or during an interaction. In the second the short and long chatter form a group, the most characteristic feature of which is that they occur after an interaction has taken place. The third group, consisting of the growl and brief chatter, is intermediate to the first two groups.

A similar and parallel transition is apparent for the function of the calls. Screeches, grunts, growls, brief chatters, and, to a certain extent, short chatters seem to express an aggressive tendency of some degree and therefore function as threat behaviour. The degrees of this aggressive tendency, and hence its threat function, does differ. For instance, a screech appears indicative of the strongest aggressive tendency, and functions as offensive threat; a grunt appears to be a threat given in a situation where the possum is startled, and apparently not had time to decide whether to attack or flee; whereas a growl or brief chatter, particularly if given after an encounter, appears to express annoyance in which an aggressive tendency is counterbalanced by some other tendency, such as fear or the mother-juvenile bond. The function in the latter case appears to be a form of ambivalent restrained threat, because although the animal appears to be threatening, it also appears to be restrained from attacking. It is not defensive threat in the sense used by Ewer (1968 p.154) because the calling possum appears to be in very little danger of being attacked by the other individual involved in the interaction.

A shift in function from a form of threat to an alarm signal, occurs with the short chatter. However as already described this shift may be a shift in emphasis, rather than any total change. An element of threat still remains in that a chattering possum looking down at a cat, is in virtually the same context as one involving another possum.

Finally, although the function of the long chatter was not determined, it occurs in the same type of context as the short chatter, except that characteristically it occurs after mating, whereas the short chatter only rarely occurs then.

It is evident therefore, that not only do these calls form a related group structually, but they also form a related group with transitional forms in both their contextual and functional affinities.

4.157 Zook-zook and Squeak

4.1571 Zook-zook

No distinctions were made between the zook-zook and zick-zick calls, until after the field observations had been collected and when the calls were analysed on the sonograph. In this section therefore, the term zook-zook covers both types of call.

4.15711 Context

In the field the call was heard 11 times, either as a single phrase or as bouts of several phrases. In all cases a dependent juvenile was present, and if not actually with its mother the mother was in the vicinity. Twice an adult male was also present. In nine of these observations it was possible to identify which individual gave the call. In eight it was the juvenile, of either sex, four between the ages of 154 and 189 days, and one 298 days old who gave rather an atypical call. The ninth observation was a call given by an adult female. On all occasions, except one, the context was one in which a juvenile became separated from its mother. Usually the juvenile was at an age when it was still riding on its mother's back, but beginning to leave it to make exploratory forays away from her. In one example the juvenile moved away from its mother and crossed into the next tree, but when only about 2m away began to give frequent zook-zook calls. On another occasion the female at Tyne St. jumped onto the roof of the house from an overhanging tree, and disappeared over the ridge, leaving her dependent juvenile in the tree. The young one became agitated and ran up and down the branches, jumped onto the roof, then back into the tree, all the time giving zook-zook calls. Eventually it went over the ridge and found its mother. On a third occasion Female 37 was sitting very low in a tree, and allowed me to lift off her back her dependent juvenile, who immediately gave a zook-zook. Its mother reached out and caught hold of my arm with her front paws, and appeared to be about to climb onto my arm, so I put the juvenile on her back. When removed a second time, the juvenile again gave a zook-zook

to which its mother immediately gave an answering zook-zook, and began to climb down towards it. The female caught hold of my outstretched arm and the juvenile climbed onto her back. One of them started clicking.

Similarly when joeys were removed from the pouches of their captured mothers they often gave zook-zook calls, sometimes while still attached to the teat, the youngest to do so being 49 days old.

The one context which differed from the above was on the occasion when Female 6147 briefly chased her 298 day old independent juvenile, who gave a call which was a cross between a harsh zook-zook and a hiss.

4.15712 Response

In the field the most marked response to a zook-zook call was that shown by Female 37 when her juvenile was removed from her back. Not only did she reach out towards her young, but she also answered one of its calls with a zook-zook. A zook-zook was given by another female in answer to a zook-zook given by her 139 day old juvenile when it was taken from her for measuring. In both these examples the zook-zook given by the female sounded identical to those given by the juveniles.

The response of a mother to her juvenile's zook-zook calls was once used to trap the female. Jill's 6½ month old offspring was placed in a cage in a large trap at the foot of her den tree at dusk, and it moved about in the cage giving loud zook-zook calls which could be heard 60m away. Jill, after numerous pauses on the way down her den tree, eventually trotted across to the trap and entered it.

Another apparent response was shown by a female who followed her calling juvenile along a branch, and another female showed signs of mild agitation while staring down at me when her juvenile gave a zook-zook call.

At times the female showed no response although any possible response may have been inhibitated by my presence, because females with dependent juveniles appeared unusually shy. However, in at least one instance - the one at Tyne St. - the female appeared to deliberately ignore her calling juvenile. She had a piece of apple which her juvenile

was trying to take from her, but she appeared reluctant to share the apple. Her rapid move to the other side of the roof appeared to be a deliberate attempt to avoid the unwanted attentions of the younger possum.

Once a very definite response was shown by Victor to the zook-zook calls given by Cloe's 138 day old juvenile, who had been placed on the cage floor. When the young possum began calling Victor jumped down from his den box and gave a shook-shook call and 2-3 clicks as he approached the young possum. First he sniffed at, then began to nibble the juvenile, and finally had to be restrained from biting it.

4.15713 Function

The zook-zook call is mainly but not exclusively given by dependent juveniles. Both the contexts of the call and the responses to it by other possums indicate that the zook-zook is a juvenile "distress" call which functions to attract its mother. However, the zook-zook calls given by females in answer to calls by their juveniles, and the response by males, suggest that the call is one of general attraction and not specifically the attraction of a mother by her juvenile.

The atypical zook-zook given by Female 6147's juvenile when chased, may reflect ambivalent behaviour of defensive threat and of juvenile distress.

4.1572 Squeak

Squeaks were sometimes made by very young joeys while still attached to the teat. The squeaks which were taperecorded were from a 54 day old joey, and the call is obviously an early stage in the development of the zook-zook call. It is doubtful whether it has any functional significance because it is made by joeys who are still permanantly attached to the teat. It is possible however, that the call may be given when the joey is uncomfortable e.g. dirty, hungry, cold or being squashed by the mother, and that the mother may respond by moving or washing the joey. However, since the behaviour of joeys of this age was not observed in this study, except when being measured, any possible function remains speculative.

4.158 Shook-shook

The shook-shook is a very soft call and few (16) were heard during the general observations of 1966 and 1967. Many (159) however, were heard during the 1968 courtship observation period, when observations were made while much closer to the possums. However, under similar observational conditions during the mother-juvenile observation period of 1968, again very few (10) shook-shook calls were heard. Although the two 1968 observations periods are not strictly comparable, they do suggest a seasonal distribution of the shook-shook call with most occurring during the main mating season.

Despite the call's striking similarity to the zook-zook, there was little confusion in distinguishing the two because of the shook-shock's lower pitch.

4.1581 Context

With 67 of the 185 observations the possum giving the call was identified. In all 67 it was an adult male. Moreover in all 185 observations there was an adult male present, and at no time was there any idication that any possum but an adult male gave the call.

Ten contexts are recognised.

(i) Male climbing tree (30 obs) A male gives a shook-shook as he climbs a tree, usually to join an oestrous female in her den tree. For example, when Victor was courting Female Dim-right-eye, he came out of his den in the cat shed and crossed 25m of bare ground to Female Dim-right-eye's den tree, usually pausing before climbing it. I carefully watched this sequence 4 times, from the time that he was on the ground at the shed. In all 4 he gave the call, but never while on the ground. The earliest that he gave the shook-shock was as he sprang onto the base of the den tree, and the latest was as he walked along the den spout to the female's den entrance. Later, after he had lost interest in Female Dim-right-eye, he continued to show sexual interest in her 12 month old juvenile. But in three observed sequences where he climbed to join the young female, Victor did not give the call, although he did when actually following her.

Six records were made of a male giving the call as he climbed an empty tree. All six however, were given by Male 22 on two separate

nights as he climbed higher up his own den tree to cross into a contiguous tree, where he had been in the habit of joining Female 24 as she crossed from her den tree. Although alone in his den tree when giving the calls, he was in effect climbing the tree to join an oestrous female. Another possibility which can not be discounted is that a male gives a shook-shook when leaving his own den tree during the courtship period. Unfortunately the observations of Victor did not include the period when he was actually coming down from his den.

(ii) Male at female's den (5 obs) A male may give a shook-shook either as he sits at the entrance of a female's den waiting for her to come out, or as he actually enters her den to join her. On one occasion the male gave the call as he entered a vacant den, but an oestrous female had left the den less than half an hour before.

(iii) Male approaching female (23 obs) When a male has joined an oestrous female he keeps within about 3m of her, and frequently approached closer only to withdraw again. As he approached closer to the female a shook-shook call was often heard. If the male had been sitting watching the female the call was given just as he moved to begin the approach, and also as he walked towards the female.

(iv) Male giving-way to female (16 obs) Having approached an oestrous female a male usually turned round, often in response to a threat given by the female. As he moved away from her a shook-shook, usually the fast variation, was sometimes heard. Similarly, if the female approached the male the call was sometimes heard as he turned to give way before her and as he was actually giving way.

(v) Male following female (15 obs) When a male followed an oestrous female, usually keeping within 3m of her, the call was often heard.

(vi) Male looking at female (8 obs) A male will sometimes give a shook-shook call while sitting within 7m of a female and staring intently in her direction. On one occasion a male gave one shook-shook while sitting watching a courting pair, who were giving frequent shook-

shook calls. He was 7-8m from them.

This context differs from the previous five in that the male was sitting still, whereas in the others he had either just started to move or was walking.

(vii) During fight (3 obs) Three shook-shooks were given during a brief scuffle between a male and female.

(viii) After fight (10 obs) More often a shook-shook was given after a scuffle as the male moved away from the female, but while still within a metre of her. In this context it was the fast variation which tended to be given.

(ix) Male on ground (1 ob) Once a shook-shook was given by a solitary male (Male 22) while on the ground, but his subsequent actions suggested that he was aware of a female, with another male, about 30m up a tree 30m from Male 22. Male 22 was wandering rather aimlessly about on the ground well outside his usual home range, and as he passed within 5m of me he gave a quiet shook-shook. Soon after this he climbed the tree next to the one containing the pair. What suggested that he was aware of the female's presence, was the fact that he was well outside his usual home range and that he tried to join her soon afterwards.

(x) Miscellaneous (8 obs) The most outstanding feature of the contexts is that 88% of the shook-shook calls were given when a male was with an oestrous female. Even the remaining 12% probably fall into this category because although the sexual phase of some females was in doubt none were definitely in anoestrus, and the calls given by a solitary male were made not long before he joined an oestrous female.

A second noticeable characteristic of the call is that it is frequently given just as a male begins to move. For example when at the foot of a tree a shook-shook may be given just after he springs onto the base to start climbing. When sitting watching a female, he calls as he takes the first steps to approach her, or as he turns to move away from her. Most other shook-shocks are given as the male is actually moving and rarely when he is stationary.

The fast variation of the shook-shook tends to be given as the male moves away from the female, either after he has approached then turned to move away, or after a scuffle with her.
Finally, as already mentioned, only adult males were ever heard giving the call.

4.1582 Response

No immediate response to the shook-shook call was detected. However, by the end of a 30 day courtship period during which the consort male continually gave shook-shook calls, the female is less aggressive towards the male (see Chapter 5). It is possible that a reduction in the female's aggression is in part a long term response to the shook-shook calls.

4.1583 Function

Since the call is given by a male when with an oestrous female, particularly when approaching her, it appears to be a courtship call. The possible long term response of the female strengthens this suggestion. The shook-shook's similarity in structure to the zook-zook suggests that it may have a similar function. If, as suggested, the zook-zook call induces the approach of another possum then the shook-shook, although not actually inducing the approach of the female, may cause her to tolerate the approach of the shook-shooking male i.e. the call may have an appeasement function. By imitating the juvenile distress call, the male may reduce her aggression by, as Ewer (1968a p.232) puts it, "...cashing in on the female's protective response towards her young...". In her review of the literature Ewer (1968a p.232) reports several examples - red squirrel, field mouse, hamster, and some canidae - of the courting male giving calls which resemble the distress calls of the young.

4.159 Click

Clicks were heard only six times in the field, not because it was a rare call, but because it was a soft call carrying less than 10m.

4.1591 Context

Five series of clicks were given in the general context of a male keeping close to an oestrous female. In four the male was either approaching or giving way to the female, and three of these were closely associated with shook-shook calls. The fifth series of clicks was made by a male as he sat on a branch 0.5m from a female between short bouts of mounting in which intromission was not successful. In three of these series it was definitely the male making the clicks while in the other two the source was not pinpointed. Similarly in the cage it was Victor who gave the clicks as he followed Cloe. When following a female a male may give the clicks at a rate of about 10 per minute, in bouts ranging in length from 1 to 24 clicks, (no. 19, mean 8.68, S.E.1.28), the clicks in each bout being very evenly spaced as already discussed in the structure of the call.

The remaining observation was made in a completely different context. I had lifted Female 37's dependent juvenile off her back which stimulated zook-zook calls from both the joey and the female as already described. When finally the female moved away with her juvenile clinging to her back one of them gave a few clicks.

Both adult males and females occasionally began to click as they came out of anaesthesia. Although not recorded on tape these clicks sounded identical to clicks made under natural conditions.

Jones (1921) records the male as making these clicks during the breeding season but he never heard a female produce the sound. Similarly Kean (1967) notes that sexually active males give the click, but he also heard oestrous females make the sound, although infrequently. He also noted background clicks given during chatters.

4.1592 Response and function

Although no direct response to a click was observed, the contexts suggest that its function is to do with courtship behaviour, particularly as it is closely associated with the shook-shook. Like the shook-shook it may have an appeasement function, but there is no direct evidence for this. Thomson and Pears (1961) on the other hand, state that the click is produced when either sex of T.caninus or T.vulpecula is faced with an unusual situation.

This suggests that the causal factor is tension produced either by an unusual situation or by an approach within the individual distance of another possum as in the case of a courting male.

A similar buccal sound has been observed in two other marsupials. One; The North American Opossum (Didelphis marsupialis virginiana) makes a metallic sounding click with its lips, which, like that of T.vulpecula, is regularly spaced but with a longer time interval between each click (4.1±SD 0.37, McManus 1970). Both sexes of Didelphis make the sound. Males click most frequently when with a sexually attractive female, but it is not restricted to the time of mating, because other situations, such as the introduction of a strange male into the cage, will stimulate clicking (Reynolds 1952, McManus 1970). Females click most frequently at the time when the young are beginning to leave the pouch. Reynolds (1952) observed that young respond to the mother's clicking by approaching her and either enter the pouch or cling to her, and that if a mother left her den without clicking the young remained in the den. McManus (1970) on the other hand, detected no response of the young to their mother's clicking. Two; The Red Kangaroo (Megaleia rufa) makes a clicking sound which is produced by movements of the tongue and lower jaw (Sharman and Calaby 1964). Two types of clucking have been recognised (Sharman and Calaby 1964, and Russell 1970b). Firstly, "a soft clucking" given by males during sexual following of a female, and also during agonistic encounters with other males. Secondly, a "loud clucking" given by a female when calling a young which was calling her. Loud clucking was also given by two hand reared juveniles when disturbed by strangers, or when fed, especially when hungry, and some by disturbed adults (Russell 1970b).

When comparing the three marsupials, all show frequent clicking or clucking by the male when sexually aroused. A second feature which is common to both Didelphis and Megaleia is that the sound is made by females apparently calling to their young. T.vulpecula does not show this but there are some observations which indicate that the female does click, and that she may do so when she has a juvenile. Kean (1967) reports that some oestrous females

clicked, though infrequently. He also mentions "smacking of the lips" (possibly synonymous with clicking) a sound given when feeding and which he claimed induced other possums, especially offspring to approach. My observations indicate that females may click when recovering from anaesthesia, and that either Female 37 or her juvenile clicked when reunited. It is possible that female clicking in relation to her juvenile may exist in T.vulpecula whether as a rudimentary behaviour, or as one that easily escapes detection, or that lip-smacking as mentioned by Kean is the equivalent to the sound in Didelphis and Megaleia. All three marsupials are also reported as making the sound at other times, especially in stressful situations, such as the introduction of a strange individual to a cage.

It is possible that this buccal sound is widespread amongst marsupials, because sounds of a repetitive structure given in similar contexts have been described, but have not been distinguished as being either buccal or vocal in origin.

Sexually excited males of two dasyurids, Sminthopsis crassicandata and Antechinus flavipes, give calls described as a short "da-da-da-da" and "cha-cha-cha-cha" respectively (Ewer 1968a 204,205). A small macropod, Bettongia lesueuri, has a call described as "thk-thk-thk", which is given by the male when sexually excited (Stodart 1966), and the males of another 3 macropods cluck when following an oestrous female (Sharman, Calaby and Poole 1966). A young captive female banded anteater (Myrmecobius fasciatus) was once heard to give a series of "tut-tut-tut-tut-tuts" (Fleay 1942). Lastly Fleay (1947 p.54) describes "huc-huc" or "hic-hic" conversational noises given by one of the large phalangerid gliders, Petaurus australis when facing a torch beam or in response to the arrival of another of its kind.

Ewer (1968b) considers that the sound given by the male Sminthopsis crassicaudata when sexually excited has no signal value and was simply a reflection of the male's highly excited condition. However, the lack of observable response does not automatically rule out a signal function. If, as is the case with the possum click, there appears to be a definite causal relationship then the call can come to signify a certain state of behaviour in

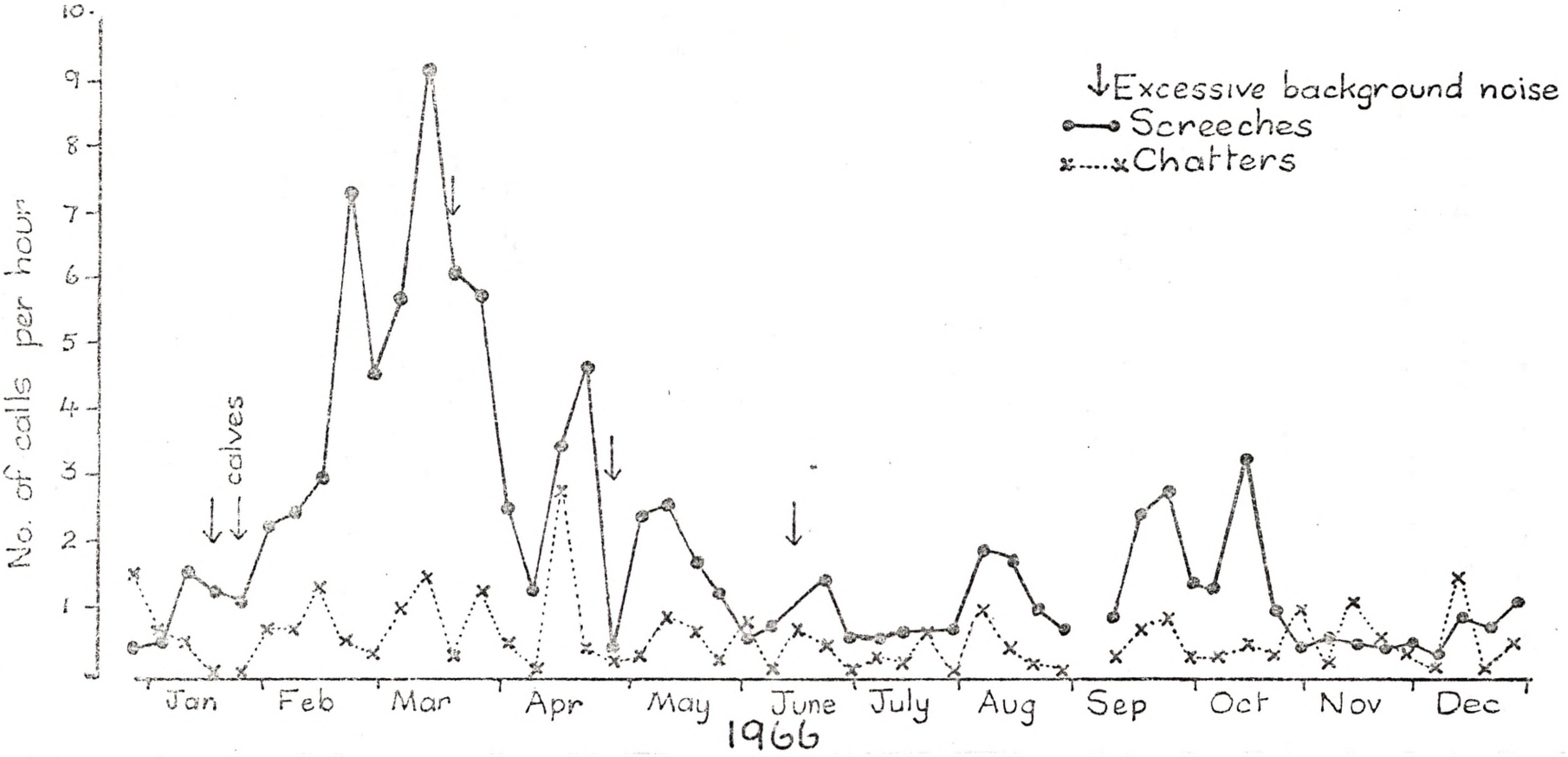


Figure 4.24 : Seasonal distribution of screeches and chatters recorded during the 1966 all-night observations.

one animal, to which another animal can respond accordingly, even if the response is a subtle one which cannot be detected by the observer. Also the reported response of Didelphis young to their mother's clicking shows that in at least one marsupial clicking does have a social function.

It is suggested therefore, the clicking made by a sexually excited male T.vulpecua has a similar function to the shook-shook call, i.e. appeasement.

4.16 Seasonal and Nocturnal Patterns of Calls

Sufficient numbers of screeches and chatters were obtained during the 1966 all-night observations to show seasonal and nocturnal patterns. All variations of the screech and hiss were combined for this purpose, and a long bout of screeching interrupted only by grunts or growls was recorded as a single screech. Similarly brief, short and long chatters were combined. Two chatters coming from the same apparent source were recorded as separate chatters if separated by one minute or more, which effectively distinguished discrete bouts, except in some long chatters.

A high level of background noise (e.g. high winds, and the bellowing of weaned calves), probably adversely effected the number of calls on four nights. Two were in January thus possibly significantly depressing the January result.

4.161 Seasonal

The frequency of screeches rises rapidly through February to reach a peak in mid-March, then decreases until by the end of May the frequency is back to the pre-February level (Figure 4.24). The low frequency continues until August when there is a second but far less pronounced increase through to mid-October, when they decrease to a low level again. This seasonal pattern corresponds to the two main breeding seasons and the mid-March peak in particular corresponds to the distribution of conceptions rather than births (Chapter 3), and as discussed in Chapter 5 screeches occur predominantly during male-female interactions during courtship.

Chatters, on the other hand, show virtually no seasonal fluctuation (Figure 4.24). This suggests that they are not correlated with breeding

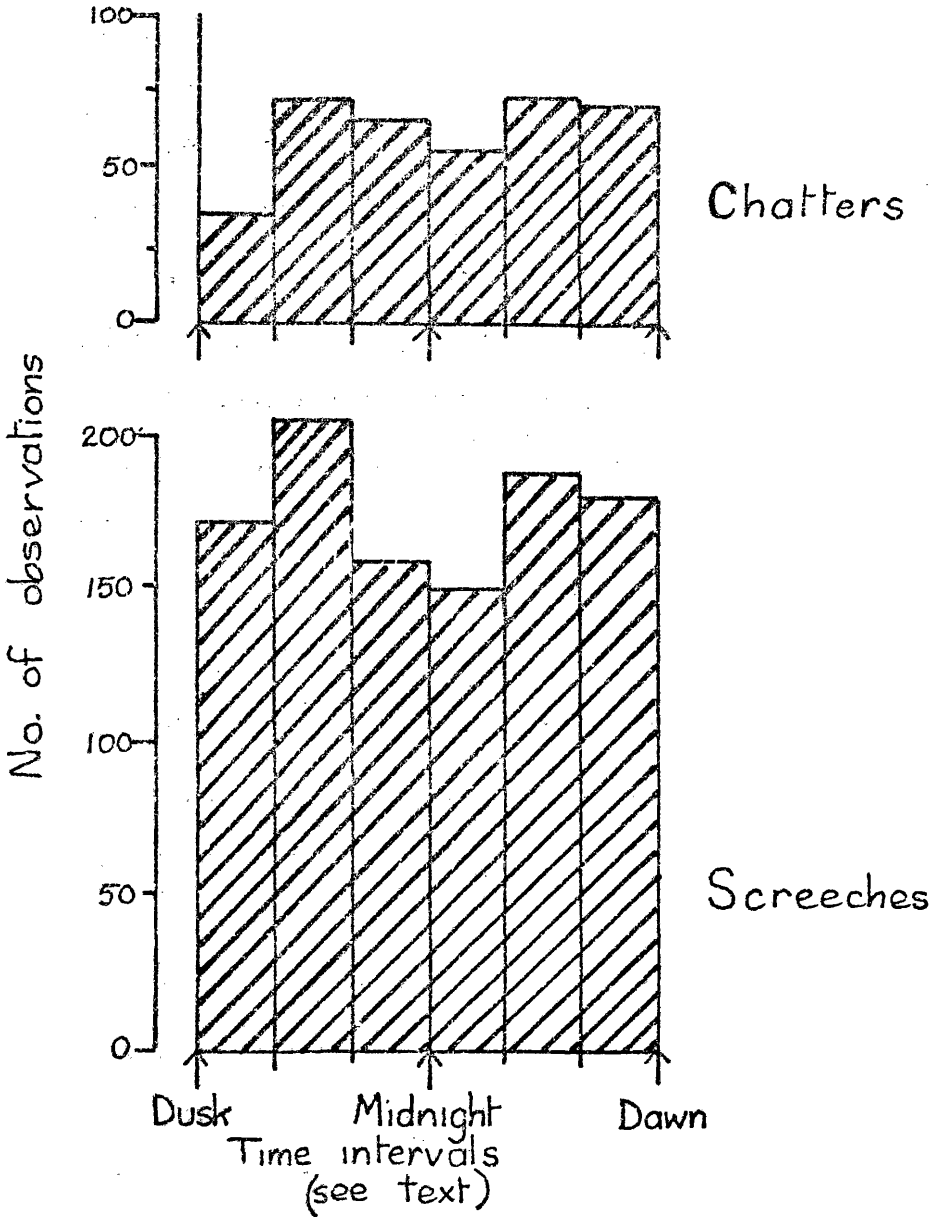


Figure 4.25 : Nightly distribution of screeches and chatters recorded during the 1966 all-night observations.

behaviour, but it must be remembered that the three types of chatter are not distinguished. The function of the chatter as an alarm signal is consistant with the lack of seasonal fluctuation. Brief chatters may easily have been masked by the screeches, with which they occurred. Long chatters, because they predominantly occurred only after mating, would be infrequent and easily missed by the once weekly observations. The peak in April may in fact represent one such series of long chatters similar to that described when four males mated with Eve in the one night. The shook-shook may also have pronounced seasonal peaks corresponding to courtship activity, as suggested previously.

4.162 Nightly

To overcome the seasonal differences in night length three reference points were taken (dusk, mid-night, dawn) and the night divided into six equal parts, three between dusk and midnight, and three between midnight and dawn. Thus the intervals for the longest night were about 1 hr. 57 mins., and for the shortest about 1 hr. 26 mins.

Both screeches and chatters show the same frequency distribution (Figure 4.25). The frequency is high during the first two and the last two intervals, especially the second, of the night. A relatively low frequency particularly during the interval after midnight separates the two modes. This frequency distribution corresponds to the general pattern of activity of the possums in which two peaks of activity are separated by a relatively inactive period during the middle of the night when much of the time is spent dozing or even sleeping on a branch (Chapter 3). No seasonal changes of distribution of calls throughout the night were detected, apart from the total number per night as discussed previously.

4.17 Discussion

In a comparison of auditory repertoires with other species it is more useful to compare the type and function of auditory signals, rather than the actual size of the repertoire which may suffer from a serious source of error if one tries to subdivide one continuously variable mode into discrete categories (Marler 1965). Differences of opinion on subdivision are not

easily resolved because, although Altmann (1965) considers that "One divides up the continuum of action wherever the animals do", Struhsaker (1967) points out that such an approach "...does not permit the distinction between the variations of one behaviour pattern all of which have the same communicative function and a graded or continuous system of behaviour patterns, in which there are an infinite number of communicative functions". He suggests an approach based on natural units as suggested by Altmann and upon the communicative function of behaviour patterns. Marler (1965) distinguishes between discrete and graded signals, and suggests that there may be a basic functional difference between the two types (Marler 1967). Thus the size of a repertoire, whether signals are graded or discrete, and the functional significance should all be examined before a true appreciation of an auditory repertoire can be obtained.

The 24 sounds in the repertoire of the possum consist of 18 definite vocalisations, 1 buccal sound, and 5 miscellaneous sounds which appear to lack any communicative function.

Both graded and discrete signals are present. A majority of the vocalisations form a group of two inter-connected series, the grunt-growl-chatter series and the hiss-screech series which are connected by a number of complex calls. The remaining vocalisations and the buccal click form a group of discrete calls despite the presence of a number of variations such as the fast and slow variations of the zook-zook and shook-shook, but the transition is rapid and no intermediate calls were recognised. Similarly, although the zook-zook and shock-shook are similar in all respects except pitch no intermediate forms were recognised. However, there may be ontogenetical transitions between the latter two not examined in the present study.

Functionally the calls can be divided into two main groups which closely parallel the structural groups. First are the calls which are basically concerned with causing withdrawl of another individual i.e. which have at least some element of threat. The degree of type of threat varies considerably, with low and high intensity offensive threat, incipient threat, startled threat, and restrained or ambivalent threat. These various forms of

threat grade into each other to form a series which parallels the structurally graded series to give an agonistic group of calls similar to that in rhesus monkeys (Macaca mulatta) observed by Rowell and Hinde (1962). Even the alarm call function of the short chatter appears to have an element of threat in it. Whatever the function of the long chatter may be, it forms a continuum with the short chatter and is therefore likely to be related in function, unless it has become emancipated from its evolutionary origin.

Secondly there are the calls which encourage or allow individuals to approach one another. The juvenile distress zock-zook and the male courtship shook-shook are the most obvious of these. Although the function of the click is not entirely clear it appears to fall into this group, especially if the lip smacking described by Kean (1967) does prove to be a form of click equivalent to that given by female Didelphis and Megaleia when calling their young.

It is not surprising that calls which are diametrically opposed in function should be clearly distinguished from each other in structure, and that calls of similar function should either grade into each other or be similar in structure.

A large group of graded calls allow for an infinite range of motivational information and one which may be a function not of phyletic level but of the degree of social integration of the species concerned (Rowell and Hinde 1962). Also the recognition of the finer shades of meaning is unlikely to be innate but learned from experience (see Ewer 1968a: 351 for general discussion). The implication here is that discrete calls are more adapted for innate recognition and for an all or nothing response. Certainly in the case of the possum juvenile distress call instant recognition and the correct appropriate response is more adaptive than any finer shades of meaning.

If the degree to which calls are graded is an indication of the degree of social integration, then the possum has a social system based on agonistic encounters in which the maintenance of a minimum distance is highly developed. On the other hand calls which represent close contact between individuals are more stereotyped and fewer in number, suggesting that the range of

situations in which individuals need to be in close proximity with each other is poorly developed, unless visual or olfactory signals are used instead.

Apart from T.vulpecula the auditory repertoire of three other marsupials is sufficiently well known for a comparison to be made. Both the North American opossum (Didelphis marsupialis virginiana) and the red kangaroo (Megaleia rufa) are relatively well known marsupials both from field and cage studies, and although the only behaviour studies have been on animals in enclosures there is a broad spectrum of knowledge making ommisions less likely (Didelphis - Lay 1942, Hartman 1952, Reynolds 1952, McManus 1970. Megaleia - Sharman and Calaby 1964, Russell 1970a & b, Frith and Calaby 1969 for general summary). Recently Macropus parryi has been the subject of a field study into its social ethology (Kaufmann 1974). Behaviour repertoires based on enclosure studies only are more likely to contain omissions. For example neither Kean (1967) nor myself ever heard a caged T.vulpecula chatter. Similarly Stodart (1965) in an enclosure study of Perameles nasuta mentions no vocalisations, presumably because they made none, but in the field this bandicoot gives a loud sneeze-like "zit" alarm call (personal observations). (See also Kaufmann and Kaufmann 1963, and Rowell 1967 for discussions on the effect of captivity on behaviour).

T.vulpecula, Didelphis, and the two macropods have certain calls in common. (1) A variety of hisses, screeches, grunts, growls and snorts are given in agonistic situations, and although they do differ from one species to the other they appear to be analogous if not homologous. This type of call is widespread amongst marsupials - see Myrmecobius fasciatus (Calaby 1960), Sminthopsis crassicandata (Ewer 1968b), Beltongia lesueuri (Stodart 1966), Schoinobates volans (Fleay 1947), and Petaurus australis (Fleay 1947). (2) A buccal click or cluck given by sexually aroused males and by females with young, though a female possum was heard to give the call only once. As previously discussed, this type of call also appears widespread amongst marsupials. (3) A variety of calls is given by the young which are described as sibilant hisses, modified screeches, squeals, squeaks, and zook-zooks, which like the first two groups are widespread amongst marsupials.

T. vulpecula has two calls however which appear to have neither analogous nor homologous forms in Didelphis or the two macropods. One is the soft shook-shook given by the courting male. This appears to be definitely lacking in Didelphis, but until a detailed examination, with sonograms, of the calls of macropods is made one can not be certain that it does not posses a similar call. After all, neither Jones (1921) nor Kean (1967) recognised the call, and the only previous reference was an aside by Fleay (1947: 40) when he compared snuffling calls of Petaurus australis to, "....sounds which were reminiscent of the soft talking notes of a male possum (Trichosurus vulpecula)." The second call possessed by T.vulpecula but not by the other two is the chatter. This is a loud call which appears to be totally lacking from the repertoire of the other three. Calls homologous to the chatter of T.vulpecula are given by some other members of the phalangerid family. Trichosurus caninus has an almost identical call both in volume and structure but with a slightly lower pitch (personal obs). The ring-tail possum (Pseudocheirus peregrinus) has a call which though quite distinct is obviously homologous. It is a subdued chatter (Troughton 1962 p.107) with very limited carrying capacity when compared with that of Trichosurus. It was once observed given immediately after the spotlight had been swung away from the ring-tail possum i.e. in a context identical to one in which T.vulpecula chattered (personal obs).

One of the most vocal of marsupials is the Yellow-bellied Glider (Petaurus australis)which has three loud calls equal in volume to the louder calls of T.vulpecula. (Fleay 1947, Wakefield 1970). One is a loud "Cha-roo-ka" given at the beginning of a glide and like the possum chatter sometimes provokes responses of the same call from other individuals. A second, described by Fleay (1947) as a whirring moan and by Wakefield (1970) as a deep-throated humming is given at the beginning of a glide. The third call is a gurgling cry which rises and falls rapidly in both pitch and volume and often follows the humming note in a glide. Nothing is known of the structure or the function of these calls so they may or may not be either homologous or analogous to the chatter. It seems probable that they function to keep individuals in contact with one another as they glide from tree to tree.

The gurgling shriek attributed to another large glider Schoinobates volans (Fleay 1947) is considered to be an erroneous observation of a call that belongs to Petaurus australis (Wakefield 1970). Certainly during many hours of spotlighting in the haunts of Schoinobates around Brisbane I have never heard the glider call.

The closely related possums and gliders have the richest vocal repertoire of marsupials in general, and there appears to be a trend for some members to develop loud calls e.g. T.vulpecula, T.caninus, and P.australis and for others to have only soft calls e.g. P.peregrinus and S.volans. This is not merely a function of size because S.volans is larger than P.australis, and as a group the five species are roughly the same size. The dilated thyroid cartilage of T.vulpecula (see Appendix III) is indicative of an evolutionary selection for a loud voice, whereas the soft voiced P.peregrinus shows no such modification of its larynx for a resonating chamber.

From the little that is known of the social organisation of the two large gliders, P.australis often travels in pairs at night, whereas Schoinobates would seem to be a far more solitary and sedentary animal. Thus the loud calls of the former may function to keep the pair together whereas no such pair contact behaviour is needed for the latter. Conversely T.vulpecula is apparently a more solitary animal than P.peregrinus in which the male-female pair bond is maintained after the birth of the joey (Marsh 1967). P.peregrinus produces a high pitched chirruping twitter while moving about feeding at night (Thompson and Owen 1964) which may be a contact call between the pair. Whereas the calls of T.vulpecula are apparently more adapted for distance communication, or to increase the volume and hence the threat aspect of vocal communication. However, until a more thorough examination of the auditory behaviour of these species is made, speculation on comparative functions remains extremely tentative.

4.2 OLFACTORY BEHAVIOUR

4.21 Introduction

As in the case of auditory behaviour it is the pragmatic meaning of a scent signal that will be considered. Similarly contextural analysis and

response of conspecifics to a scent signal will be used to deduce the social function of olfactory behaviour.

There are some important differences between auditory and olfactory signals. Firstly an auditory signal dissipates rapidly and a response to the signal is assumed to be immediate. An olfactory signal on the other hand may remain long after it is deposited on a substrate. Therefore a response to the signal may occur in the absence of the animal giving the signal. Even an air born scent may dissipate much more slowly than an auditory signal. Secondly an individual giving an auditory signal has proprioceptor feed back from its lungs, larynx and buccal cavity which enable it to distinguish an auditory signal made by itself from a similar signal made by another individual. With a long lasting olfactory signal if it is to act as anything other than a general species scent, an individual must be able to distinguish at least its own scent from that of other individuals from the properties of the scent alone. There is no proprioceptor feed back except at the time of depositing or emitting the scent. Thirdly there is the difficulty of a relatively anosmic human observer being able to detect the actual signal. Instead one has to rely on behaviours which are associated with the deposition or emission of scent, such as substrate rubbing and the sight of a fluid medium.

Jones (1921) after his preliminary study of the behaviour of the possum concluded "As is not at all unnatural in an arboreal animal, the sense of smell is by no means highly developed, and it seems to be of little importance in obtaining food or in avoiding enemies". Subsequent authors have however described a number of glands associated with olfactory behaviour. a longitudinal median ventral line of brown fur on the sternum marks the site of concentrated sebaceous glands and is known as the "sternal gland" (Bolliger and Carrodus 1938). It is particularly well developed and has a greasy appearance in males (Bolliger and Hardy 1944). The gland is a secondary sexual character as demonstrated by Bolliger and Hardy (1944). Rubbing of the sternal gland on projecting objects, logs etc. has been recorded (Bolliger and Hardy 1944, Mollison reported by Thomson and Pears

1962, and Kean 1967). Bolliger and Hardy (1944) considered that its function was to attract the opposite sex by its colour and odour, and where marking occurred to guide a prospective partner. Thomson and Pears (1962) on the other hand attribute a territorial function to sternal gland marking. Kean (1967) observed that sternal gland marking occurred on new objects placed in a cage, and by captive possums when released.

Two pairs of paracloacal glands have been described in the possum. One an holocrine "cell" gland which releases cells continuously, and the other an apocrine "scent" gland which secretes a cream coloured oily liquid consisting of oil droplets emulsified in an aqueous phase and has a strong odour (Bolliger and Whitten 1948). Cells from the cell gland are liberated onto the rim of the cloaca and are either washed away by urine or as a coating on the faeces (Bolliger and Whitten 1948). These authors also found that the cells may last for several weeks in urine. Kean (1967) has suggested that the durability of the cells give urine a persistant odour. Kean (1967) also describes two methods of depositing urine which indicate that it is used an olfactory marker. Cells occur in exceptionally high quantities in the urine of juveniles of both sexes, are numerous in adult males, but extremely sparse in the urine of adult females (Bolliger and Whitten 1948). Kean (1967) has suggested that urine marking is associated with "proprietary rights". The scent glands do not release their secretion continuously but copiously for limited periods (Bolliger and Whitten 1948). The function of the strong scent of this secretion has been given as defence against predators (Bolliger and Whitten 1948, and Thompson and Pears 1962), as a territorial marker (Thompson and Pears 1962), or is associated with sexual behaviour (Thompson and Pears 1962).

4.22 Description of olfactory behaviours

4.221 Chesting

The rubbing of the sternal gland is here referred to as chesting. The gland is brought into contact with the substrate by a forward rubbing movement in which the chin is held stretched forward and clear of the substrate. The legs are bent during the forward movement but the feet remain stationary.

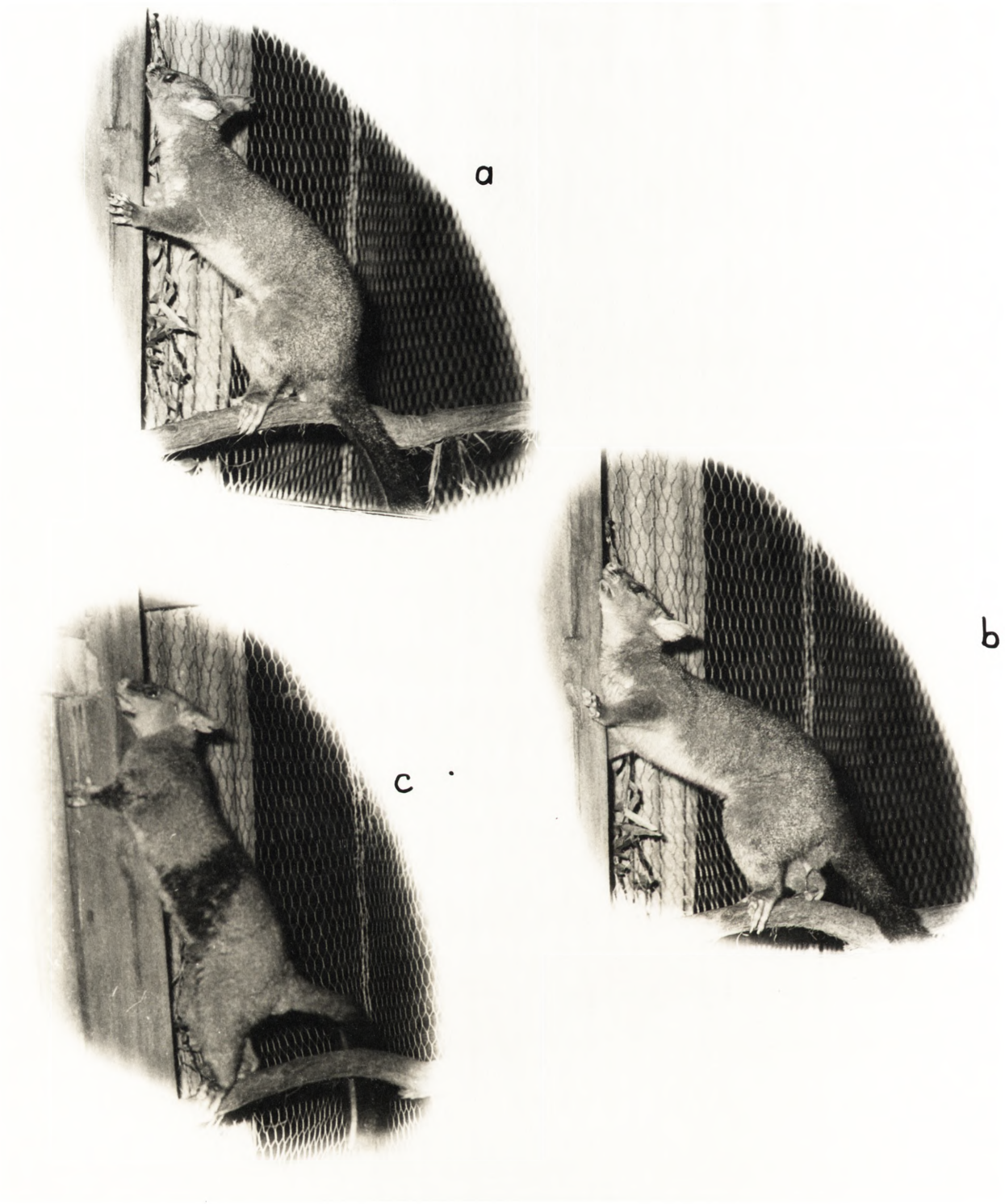


Figure 4.26 : Chesting. a) Stance adopted prior to chesting, b) the upward rubbing action, c) as for b except chest is pulled hard against the substrate by the front legs.

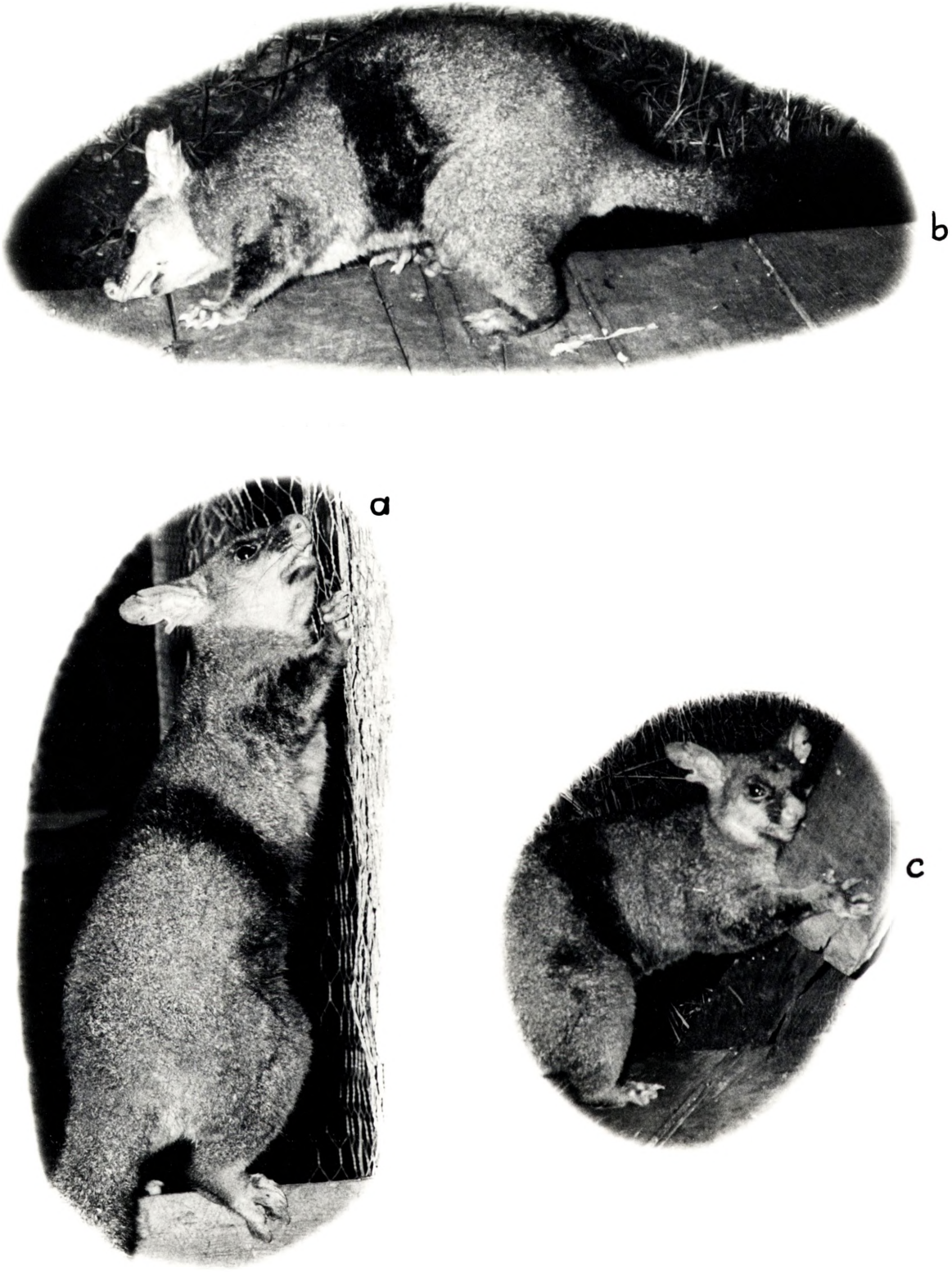


Figure 4.27 : Chinning a) Note lower lip rolled back exposing lower incisors, and chest clear of substrate; b) note rotation of head and chest clear of substrate; c) note chinning and chesting performed simultaneously.

At the end of the forward stroke the possum lifts its chest off the substrate and returns to its original position. The rubbing movement may then be repeated.

When chesting the base of a tree the possum stands or squats on the ground with both paws on the trunk at shoulder height (Figure 4.26 a-c). A maximum of three rubs per bout of chesting was observed when in this position, and sniffing the substrate after each stroke rarely occurred. Occasionally the possum climbs slowly right onto the base of the tree (not the usual leap) and may even climb 1½m before rubbing forward and upward as it clings spread eagled to the trunk. After chesting, the possum usually jumps back to the ground.

When marking thin branches the front paws clasp the back of the branch and appear to pull the chest onto the branch. Sometimes the front paws are placed high above the head rather than at shoulder height. In the study area eucalypts had thin (1-2cm diameter) vertical branches growing from larger horizontal or diagonal branches. As a possum walked along the larger branch these thin branches were sometimes chested on passing by placing one front paw at shoulder height on the vertical branch, and giving the branch a wipe with the chest.

On the ground bare earth, tufts of short grass, and fallen logs were chested. The logs were usually marked with a single quick rub as the possum either walked along or crossed over the log, and the log was not sniffed after chesting. In contrast the chesting of bare earth and grass tufts was usually thorough. The rubbing movement was firm and repeated up to an observed maximum of 12 times, either in exactly the same place without moving the feet or within a 50cm radius. Between each movement the substrate rubbed was carefully sniffed.

4.222 Chinning

A possum may rub the anterior part of its mandible on the substrate with a forward and slightly rotating movement of its head. This pushes the lower lip back and exposes the lower incisors (Figure 4.27 a). Rotation of the head may continue to bring the whole side of the head into contact with the substrate (Figure 4.27 b&c). Chinning varies from a single rapid light wipe with only slight rotation of the head, to a vigorous rubbing of the substrate

Figure 4.28 : Urine marking.
a) Upper - Cloaca held high off substrate in normal walking posture, note head held low as substrate sniffing performed.
b) Lower - Cloaca lowered to perform urine

with maximum rotation, and repeated several times, particularly when short tufts of grass or flat surfaces, such as a cage floor, are rubbed. Places chinned were fallen logs, bare earth, tufts of grass, tree bases, branches particularly the thin vertical ones, the ends of broken off branches, and den rims.

Chinning is often associated with chesting, usually performed just before chesting, but sometimes in the same forward movement (Fig 4.27 c). As a result it appears to have escaped the attention of previous authors. That it is an independent behaviour and not just part of the chesting action is indicated in Figure 4.27 a&b, in which the sternum of the possum is held well clear of the substrate during chinning.

Externally no glandular region is evident on the chin. However, histologically the lower margin of the chin, particularly of adult males has well developed sebaceous glands (W.J. Freeland pers. comm.) even larger than those described for the sternal gland by Bolliger and Hardy (1944). The glands form an almost uninterrupted layer of glandular tissue in the region of the dark patch of fur just below the lower lip (Fig 4.27 a&b).

It is possible therefore that the action of chinning deposits secretion from the sebaceous glands on the substrate. Nevertheless the rolling back of the lower lip, particularly during maximum rotation of the head, may deposit saliva on the substrate, which has been demonstrated to have communicative value in the marsupial glider (Petaurus brevicens papuanus) by Schultze-Westrum (1965). No attempt was made to resolve this problem in this study.

4.223 Urine Marking

Kean (1967) has described two patterns of urine deposition which are indicative that urine is being used as a scent marker. In one a sigmoid strip about 45cm long is deposited with a sinuous body movement, and in the other a drip trail of urine is left over a distance of many feet.

Both behaviours were observed in the present study. When leaving the sigmoid strip the possum lowers its hind quarters by bringing the hind legs forward of their normal walking position, and waddles forward with a pronounced sinuous movement of the hind quarters (Fig 4.28). A trail of urine 15 to 45cm

long was deposited. The cloaca protrudes to form a definite hillock but is not rubbed on the substrate, although the long cloacal vibrissae may touch. In the drip trail the hind quarters are lowered as for the sigmoid strip but not in such a promounced manner. Urine drips from the vibrissae of the protruding cloaca at intervals of 15 to 20cm as the possum walks forward. Sometimes the cloaca was lowered sufficiently to touch the vibrissae to the substrate.

In one observation of a caged adult male, urine was ejected in short squirts, rather than the dribble of the drip trail, leaving a trail of short strips.

4.224 Paracloacal Scent Gland Secretion

The paracloacal scent glands secrete a cream coloured oily liquid consisting of oil droplets emulsified in an aqueous phase, which is released copiously for limited periods, unlike the continuous secretion of the cell glands (Bolliger and Whitten 1948). The secretion has a strong smell which the above authors describe as "...an unpleasant odour resembling that of rotten onions or garlic.", and which Kean (1967) describes as "..not being strong but readily perceptible in small amounts." To me the scent had a strong, rather sickly-sweet musky odour which could be detected several metres from the possum, and on a substrate for at least 24 hours after deposition.

Observations of the liberation of the scent gland secretion were made on two caged males. In both males a pronounced cloacal hillock formed as in urine marking. The creamy coloured fluid oozed out of the cloaca to saturate the fur around the cloaca and collected between the cloacal vibrissae. One male never deliberately dabbed or rubbed his cloaca on the substrate, but the secretion became smeared in places where he sat or accidently touched the substrate with the cloacal vibrissae. On the other hand, the second male, on the one occasion when was seen to release the secretion did apparently deliberately deposit the secretion on a branch. He did this as he ran along a horizontal pole with his hindquarters lowered, and left two sinuous trails each 15 to 20cm long. His actions were similar to those of a possum depositing a sigmoid strip of urine, and it was apparent that only the cloacal vibrissae

touched the pole to leave the trail of scent.

4.225 Sniffing

Two behaviours are indicative of a possum monitoring scent either on a substrate or in the air.

In substrate sniffing the possum holds its rhinarium within 5cm of the substrate (see Fig 4.28 a) with the long axis of its head at about 45° from the horizontal instead of the normal 30°. When climbing the trunk of a tree a possum's nose is very close to the trunk, but with the long axis of the head parallel to the trunk. To sniff at the trunk the possum lifts its head away from the tree and points its nose directly at and perpendicular to the trunk with its rhinarium within 1cm of the bark. At the base of a tree the possum may stand on its hind legs with forelegs on the trunk as it sniffs the trunk.

Substrate sniffing may be done as the animal continues to walk, or during a pause. A pause may vary from barely a perceptible pause to a thorough olfactory exploration of an area 1-2m in diameter for up to 3 minutes.

It was difficult to distinguish sniffing from feeding on the ground, unless the possum stopped to thoroughly examine an area. Then the sniffing was usually associated with chinning and chesting of the ground or grass tuft.

Air sniffing is indicated when a possum stretches its head and neck as though reaching for a distant scent source with its nostrils. The rhinarium is practically immobile with none of the twitching actions associated with other animals such as the domestic rabbit. However, when close to a possum faint snuffling noises can be heard as the animal extends its nose.

4.23 Functional Analysis

4.231 Chinning and Chesting

4.2311 Context

In the field chinning was the harder of the two to detect. Even when performed alone chinning was more easily missed than chesting because it was a less pronounced marking movement, and when associated with chesting it was often obscured.

For the purpose of this analysis therefore chinning refers to observations

of chinning alone and not that associated with chesting, unless otherwise stated. Conversely chesting alone and chesting closely associated with chinning are lumped unless otherwise stated.

Contexts within which marking occurred are primarily considered in relation to the presence or absence of another possum in the vicinity of the marker. Vicinity being defined as being in the same tree or within 20m on the ground of the marking possum.

Observations from all periods of the study are used in the analysis, but only if the status of the individual is known, and only if it had been under observation sufficiently long for the context to have been established. Where an observation could be placed into more than one context, it was assigned to one context based on a subjective judgement as to which was the overriding context. For example a male marking his own den tree, which also contained a female, did so in two contexts, (den tree, and female in vicinity). If he went straight to his den and ignored the female the observation was assigned to the den-tree context. If on the other hand he approached the female and appeared to be interested in her then it was assigned to the female-in-vicinity context. Where no such judgement was possible the observation was assigned to a miscellaneous context.

4.23111 Adult males (302 obs)

4.231111 No other possum in the vicinity (133 obs)

Most observations (100/133) were of a male either chinning or chesting the ground or more usually the base of a tree when he was travelling on the ground. As he travels, often from his den tree to a feed tree, a male will turn aside to mark the base of a tree he is passing, perhaps sniff at it, then continue on his way. There appeared to be no set pattern of marking special trees or of following a regular route, and the amount of marking performed in any one travelling bout was low, with a mode of one and a maximum of eight (Table 4.9).

In the bout containing eight markings Gus had come down to the ground from his den tree in the evening and had travelled 305m to a tree where he had spent much of the night. The trees marked were 120,220,240,260,265,300,301

and 305m respectively from his den tree, the last being the tree he climbed. Three times he climbed right onto the base of the tree before marking, twice jumping down to continue his travels, the last time climbing the tree. In the remaining five observations he stood on his hind legs to mark the trunk. Three weeks earlier he had followed virtually the same route when following an oestrous female to the same tree, but with less marking. In the earlier of the two observations he had been acting as a consort male (see Chapter 5), but by the time of the later observation he had ceased to be sexually interested in the female.

Table 4.9

Frequency distribution of chinning or chesting (ground or tree base) performed by an adult male in any one travelling bout on the ground, during the 1966 all-night observations.

Markings per travelling bout	1	2	3	4	5	6	7	8
Frequency	13	6	6	3	-	2	-	1

Although no other possum was in the vicinity when marking actually occurred, the immediate area marked was often known or inferred to have a history of possum use. For example 17 of the 70 observations of male chinning and chesting the gound or a tree base during the 1966 all-night observations came into this category. Nine were of trees containing a den (other than the males own den) and were therefore assumed to have a history of possum use. In the remaining 8 another possum had been seen in the immediate area previously the same night. For example Jack sniffed and chested the gound and the base of a tree known to have been used by Jill 3 hours earlier. On another occasion he carefully chested the ground at least 8 times (counted as one observation) at the base of a tree vacated by Jill 5 mins earlier, and earlier the same night had chested the base of her den tree 45 mins after she had vacated it. The marking of a male's own den tree has been included in a separate context discussed later and 13 of the 26 observations were in the absence of another possum, but again because it was his den tree there was a history of possum use.

Marking performed actually in a tree as opposed to just its base (33 obs),

showed an even higher proportion of prior use by another possum of the tree.

On six separate occasions males climbed into empty den trees which were not their own, and marked the tree near the den (18 obs). During three of these occasions the males thoroughly explored the tree by carefully sniffing the branches, particularly in the region of the den. The sniffing was accompanied by chinning and chesting, more than is indicated by the 18 recorded observations because in the first of the den tree explorations the field notes merely record "..much marking performed".

The remaining 15 observations were in trees other then den trees. Of the 10 observations made during the 1966 all-night periods, 8 occurred in a tree with a history of possum use consisting of regular previous visits by possums.

Only two observations of chinning and chesting in a tree occurred without a known or inferred previous use of the tree by a possum.

4.231112 Oestrous Female in the Vicinity (119 obs)

Marking seen performed by a male in the vicinity of another possum was usually in the vicinity of an oestrous female, when, as discussed later (Chapter 5) the male was showing definite sexual interest in the female.

Marking performed in the presence of an oestrous female can for convenience be divided into three main categories.

(1) When following an oestrous female on the ground the male chinned and chested (10 obs) in a similar manner to the tree base marking performed by him when travelling alone.

A few of the observed markings however, did take place in apparent response to an action of the female. Twice after brief encounters between Gus and Gert he rubbed the base of a tree, once immediately after the encounter and once following a pause of about one minute. On another occasion Gus sniffed, then chinned and chested the base of a tree, sniffed at but not marked by Gert, possibly in response to a scent that they had both investigated. Victor, while following Female Dim-right-eye, twice chested then very carefully sniffed at bare earth where the female had stopped for about half a

minute.

The fact that marking was always done behind the female as they travelled suggests that the male is not directing his marking at the female.

(2) Marking a tree containing an oestrous female (97 obs) was relatively the most common situation, with numerous contexts recognisable in this general context.

When a male followed a female up a tree he usually chested or chinned the base of the tree (10 obs) before climbing after the female. Sometimes after marking the base of the tree he would feed or aimlessly move about at the base of the tree before following the female.

On leaving his own den tree at dusk to join an oestrous female in her den tree, he always marked the base of her tree before climbing it (15 obs). During Victor's consort period with Female Dim-right-eye, he was observed 7 times climbing into her tree to join her and her year old daughter during a 3-4 week period. The first time he did not mark the base of the tree, but did chin the rim of the female's den while she was still in it. The next five times he chested the tree base before climbing; twice climbing immediately after marking and the other 3 times moving about the base sniffing the ground after marking. Only on the last occasion did he climb the tree without any marking at all, but by this time he had lost interest in Female Dim-right-eye and was following her daughter who presumably had come into oestrous for the first time.

When joining a female at dusk who had not yet emerged from her den, a male frequently sat peering into her den and usually chinned and occasionally chested the den rim. For example Victor invariably marked the den entrance when he joined Female Dim-right-eye. Marking of the female's den entrance also took place after the female had left her den (3 obs). This was the only situation in which a male marked a place where the female would have to pass the scent mark.

The most vigorous sniffing and marking by a male occurred when

he investigated a branch where an oestrous female had been sitting for any length of time. As soon as the female moved away the male immediately moved to the place where she had been sitting, carefully sniffed, and sometimes marked the branch. Marking varied from a very quick wipe of the chin or chest on the branch to vigorous marking, usually by chinning, the spot several times. On one occasion the male vigorously chested the branch twice, each time drawing back to sniff the branch. Age, or possibly status, of the female may have an effect on the probability of marking following sniffing in the above context. There was a trend for less marking to take place when the female was a young one coming into oestrous for the first time (Table 4.10).

Table 4.10

The number of observations of male sniffing and marking (chinning or chesting) where a female had been sitting, in relation to the age of the female

	Female		
	Adult	Juvenile	
Sniffed only	20	6	26
Sniffed and marked	13	0	13
	33	6	39

$G = 2.416$, 1 d.f., $p > 0.1$ n.s.

(Yate's correction used)

This is based on a series of 6 observations in which Victor sniffed at but did not mark where Female Dim-right-eye's daughter had been sitting. The juvenile had come into oestrus for the first time, judging by the way Victor was following her with the appropriate courtship behaviour, although she was still sharing her mother's den. This marking was not directed at the female who had been sitting on the branch, because it was performed at places just vacated by her and not at places where she was likely to come across the scent of the marking male. It was the presence of the female's scent on the branch that appeared to stimulate marking by the male.

A male would also quickly chin or chest a branch as he followed a female along a branch (7 obs). This context differed from the previous context in that the marking was not done where the female had been sitting.

In a slightly different context males were observed chinning or chesting a branch (6 obs) as they approached a female from the front to come within 1½m of her, and in one of these observations Donald marked the branch as he approached Jess prior to mounting and mating with her. Approaching a female from in front is a socially more stressful situation than approaching from behind and may by a causal factor in stimulating marking as discussed later.

Similarly following an encounter with a female a male sometimes marked a branch (8 obs). The marking usually took place after the male had moved a metre or two from the site of the encounter, and in some observations the male appeared agitated.

Marking was also performed in situations indicative of conflict between approach and withdrawal by the male (6 obs). When within the minimum individual distance of about 1½m, a male often appeared undecided whether to come closer to the female with a resulting aggressive encounter, or to withdraw. In this situation a male sometimes marked the branch.

A number of observations (13) either took place well away from the female though still in the same tree, or were not clear as to their context. There was no evidence that any differed markedly from the contexts already described.

(3) A complicating factor was the presence of a second male as well as the oestrous female (9 obs). Twice the marking was done in a context involving the female, once after an encounter with the female and once he chinned where the female had been sitting. Twice the marking occurred during a definite interaction between the adult males. In one of these, two males were approaching each other and appeared uncertain of each other's status. When 1¼m apart one stopped and chested the trunk, at the same time flicking his tail from side to side. He

then continued his approach and when about 0.5m apart both males suddenly turned and rapidly moved away from each other. In the other Victor had climbed into a tree containing Eve and Donald. He had then chased Donald down the tree and on his way back up Victor paused to carefully sniff at a place where Donald had been sitting and chested a small branch just beyond. In the remaining 54 observations it was not clear whether the context primarily involved the female or the second male. There was no evidence that the presence of a second male increased the rate of marking.

4.231113 Anoestrous Female in the Vicinity (9 obs)

Males spend little time with an anoestrous female (see Chapter 5) which in itself accounts for the low number of observations in this category. In five of the observations males on three separate occasions had shown overt interest in the female but this interest had quickly waned. In one Jack had watched Jill climb the tree he was in and then moved across to a branch she had traversed and chested it, but then seemingly ignored her. In the second Gus sniffed and marked as he climbed a tree containing Hester which she had climbed earlier in the night. However, he never came closer to her than 3m and soon began to feed steadily. Similarly on the third occasion Jack had marked the trunk of a tree containing Eve, but once he had come within about 3m of her he seemed to lose all interest.

Another 3 observations took place in a tree with an anoestrous female, but at no time did the male show any interest.

In the ninth observation Jack slowly climbed Lesley's den tree, carefully sniffing the trunk, and once chinned it. Lesley was still in the tree and Jack, suddenly becoming aware of her, immediately descended the tree. The context of this observation is probably that of a male exploring a den tree other than his own as already discussed.

Several observations in which a male marked his own den tree either when he left it at dusk or when he returned at dawn, were done in the presence of a female who also had a den in the tree. However, these observations have not been included here if the male completely ignored the female. Instead they

are treated in a later contextual category.

4.23111 Adult Male Only in the Vicinity (3 obs)

Apart from the observations already described in which both a male and an oestrous female were in the vicinity, only one observation appeared directly related to the presence of the other male. Tony, who was sitting 9m up a tree, chinned a branch beside him when Victor climbed into the same tree and sat on a branch 5-6m below him. In another Donald and Jack were both feeding on the ground and moving parallel to each other in the same direction and about 5m apart without any apparent antagonism. Donald turned aside to chest a tree frequently used by Alice and climbed by her a few minutes earlier. In the last observation Male 22 chested the base of a tree frequently used by possums in the area soon after Victor had descended another tree 9m away.

Males sniffed where other males had been sitting in the same manner as they sniffed at a branch where a female had been sitting. Although the number of observations are low (6) there is a trend that a male is less likely to follow such sniffing by marking, when the scent is that of a male (Table 4.11). The only observation of marking following sniffing of a male scent occurred in the observation in which Victor chased Donald down a tree and on his way back up to mate with Eve, Victor sniffed then chested where Donald had been sitting.

Table 4.11

The number of observations of male sniffing and marking (chinning or chesting) where another possum had been sitting, in relation to the sex of the other possum

	Sitting Possum		
	Male	Female	
Sniffing only	5	20	25
Sniffing & marking	1	13	14
	6	33	39

$G = 0.382$ 1 d.f. $p > 0.5$ n.s.

(Yate's correction used)

4.231115 Juvenile in the Vicinity (2 obs)

Juveniles were frequently with their mothers when a male was marking, but it was the adult female with whom the male was interacting.

Only twice was marking observed in the vicinity of a juvenile alone. In one the male chested the base of a den tree containing a juvenile female before climbing it. He appeared to be more interested in the den and climbed straight to it, only meeting the juvenile on his way down. On the other hand in the one observation involving a juvenile male (11 months old) the adult male appeared to be performing a displacement action. Jack climbed the small tree containing Gerald, very carefully sniffing the trunks and branches, and once chinned a branch. Gerald who was 6m up the tree, became agitated and eventually dashed past Jack down the tree. Jack appeared to take no notice of the juvenile and continued to climb the tree.

4.231116 Marking Own Den Tree (36 obs)

On leaving his den at dusk a male sometimes chinned or chested the tree (12 obs). This usually took place as he moved away from his den, but once it was performed as the male sat outside the den entrance. When no other possum was in the tree the marking was always light, usually consisting of chinning as in the following observation. "Male 22 has come out of den T195 and onto a branch below the den. As he walked along the branch he sniffed at it and chinned it several times. He may also have chested it lightly". When on the other hand the male shared a den tree, though not the same den, the marking appeared to be more vigorous. Male 32 after emerging from his den vigorously chested a branch opposite his den entrance, a branch that was regularly used by Jill and her Joey on their way down the tree.

When returned to his den at dawn a male sometimes chinned or chested (24 obs) either the base of the tree, or the branches, as he climbed up to his den. These observations occurred on 14 separate occasions. On 6 it was the base of the tree that was marked, sometimes followed by further marking higher up the tree, and on 8 marking did not occur at the base. There was no particular marking place in the tree in relation to the den, except for a slight tendency to mark closer to the den used when more than one den existed

in the tree.

Like all other contexts marking did not invariably occur. However, marking of the den tree is one context in which it was possible to obtain the relative frequency of marking to non-marking occurring in a particular context. Taking the three central males it is apparent that marking occurred on about half the return trips to the den with no significant difference between individuals (Table 4.12). There was however significantly more marking performed by males than females on their return to their dens.

Table 4.12

The relative frequency of marking (chinning or chesting) to non-marking of its den tree by a possum returning to its den at dawn, during the 1966 all-night observation period.

		Den Tree		
		marked	not marked	
Adult males	Jack	3	5	8
	Gus	6	5	11
	Alec	5	6	11
	Total	14	16	30
Adult females+		4	22	26
		18	38	56

+ Three central females (Jill, Gert, Alice) only.

Independence of Individual males

$G = 0.554$ 2 d.f. $p > 0.5$ n.s.

Independence of males (combined) and females

$G = 5.080$ 1 d.f. $p < .025$+

4.23112 Adult Female Marking (31 obs)

Female chinning and chesting was never as vigorous as that done by a male, and usually consisted of a single quick light rub of the substrate. Often in fact it was doubtful whether marking had actually taken place.

4.231121 Exploring Den Tree

The most thorough marking by a female observed occurred during an exploration of a den tree. Female 6147 with her 8½ month old daughter

following first chested the base of a 3m high hollow stump of a dead tree three times. After two minutes spent feeding at the base of the stump she stood on her hind legs with front paws on the trunk and carefully sniffed at some twigs. She moved 0.5m away from the stump but returned within one minute and began climbing, followed by her daughter who sniffed the stump as she climbed. On reaching the top the female peered into the opening then moved round the rim of the hollow sniffing at it carefully. She chinned a projection twice, sniffed again, chinned another projection and nibbled a third. After sitting grooming for a minute or two on the rim of the opening Female 6147 hung head first into the cavity with just the tip of her tail hooked over the rim and was obviously thoroughly investigating the cavity. Thirteen minutes after climbing the stump she came down to the ground with her daughter following. Whilst investigating the rim her cloacal hillock was seen protruding and glistening with fluid and she may possibly have once rubbed the rim with her cloaca. Her daughter had carefully sniffed the rim, hung head first into the cavity, nibbled and may even have chinned the rim. Although no possum was ever seen to use this tree as a den, the hollow centre to the trunk made it a potential den though rather exposed to rain.

Somewhat similar in context were observations in which a female investigated a male's den soon after he had vacated it at dusk (see Chapter 5) In three of these observations the females chested close to the den entrance after sniffing it.

4.231122 Marking Own Den Tree (6 obs)

This context was the same as that observed for the males except that the frequency of marking was significantly less (Table 4.12). In one of the two observations of marking taking place early in the evening the female was accompanied by her 14 month old son and is possibly more appropriate in a following context.

4.231123 Miscellaneous Contexts

Chesting was observed four times when another female was in the

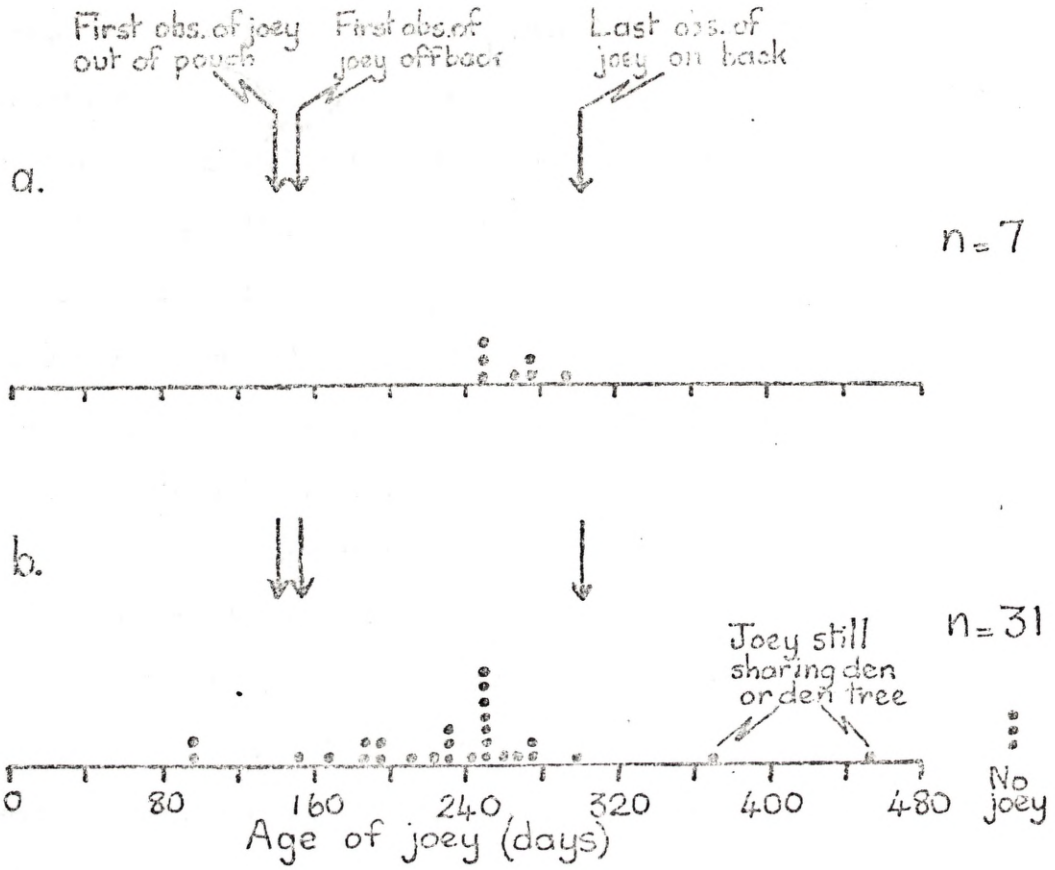


Figure 4.29 : Observations of female olfactory marking in relation to age of accompanying joey (dot = 1 obs).
a) Cloacal and urine marking.
b) Chinning and chesting.

vicinity. Gert and Hester had come within about 10m of each other and although no definite interaction took place they seemed to be aware of each other. As they moved apart Gert chested the ground at the base of the tree then the tree base itself. This was the only observation of a female marking the ground. In another instance Jess chested the base of a small tree containing Jill and her joey. Jess then climbed the tree sniffing at it very carefully. Soon afterwards an agonistic interaction followed in which Jess chased Jill to the ground where a fight took place. Jess climbed back up the tree which still contained Jill's joey, but Jill remained at the base, once looking up the tree then chesting the base, but with no attempt to reach her joey.

An adult male was in the vicinity during five of the observations of female chinning and/or chesting. Twice when the female investigated his den, once in the den tree when she investigated her male juvenile's den, and once a male was already in the den tree which a female marked before climbing at dawn. The fifth observation also occurred in a den tree. A female with a joey riding on her back appeared to rub her belly and her chest along an horizontal branch. An adult male showing considerable interest in the female was nearby.

Female marking of a tree base as she travelled on the ground was observed 6 times. Three times the female was alone with no other possum seen in the vicinity, and three times she was being followed by her joey.

Five times a female chinned or chested the branch of a tree as she descended it closely followed by her joey, in all cases it was not a den tree, although in two it was a contiguous tree. Once a female chested the base of a tree when a nine month old juvenile male was crouched 3m from her, staring at her.

A high proportion of female olfactory marking occurred between the first and last observations of a joey riding on her back (Fig. 4.29). Only 7 out of a total of 31 observations occurred outside this period and two of these occurred in the female's den tree, and in one instance her den was being shared by her son. The significance of this is discussed later.

4.23113 Juvenile Marking

The age at which chinning and chesting was first observed was 8½ months for females, when female 6147's daughter chinned the den rim during the investigation of the den tree already described, and 21 months for males. The much older age for males is most likely a result of inadequate observations rather than a significant difference between the two sexes.

In another observation the 10 month old Jess chested the spout of her den as she approached it at dawn, indicating that chinning and chesting start at approximately the same age.

No marking was observed by juvenile males whilst still living in the maternal home range, the oldest of these young males being 16 months before it dispersed. However, two males in the process of establishing themselves were seen marking. One of these, Male 6214 (22 months old), marked a branch as he emerged from a den shared with Alice, (possibly his mother). The second, Bill (21-25 months old) marked on three separate occasions. Once during an exploratory trip when he marked the base of a tree which was known to have been marked by two other males on previous occasions, once the base of his den tree before climbing it at dawn, and once following a mild alarm when on the ground.

Vigorous chinning, in fact the most vigorous seen throughout the study, was seen performed by an unidentified male whose testes were still small (i.e. less than 16 months old), but whose sternal gland appeared brown and greasy. He came into the study area one night and climbed into a tree containing 3 dens, at least one of which was used every night. He wandered about the tree sniffing the branches and occasionally chinning. An hour later he climbed into a second den tree and chinned a branch vigorously, and 15 minutes afterwards into a third den tree used by Lesley that day. As he climbed the third den tree he paused to sniff the trunk carefully. For twenty minutes he clambered about the tree sniffing and chinning branches paying particular attention to the immediate vicinity of the den where he also chewed at the wood. His chinning in the region of the den was the most vigorous, and at times he possibly lightly chested the tree. This context is

Table 4.13

A summary of contexts in which chinning and chesting (includes chinning performed with chesting) by adults were observed during the 1966 all-night observations

Marker	Context	No. of observations Chinning	Chesting	Total
Male	No other possum in vicinity			
	Travelling on the ground	9	61	70
	In a tree	4	2	6
	Exploring den tree other than own	4	6	10
		17	69	86
	Own den tree - dusk	3	1	4
	- dawn	5	17	22
		8	18	26
	Oestrous female in vicinity			
	Following female on ground	2	6	8
	In tree with female	9	13	22
	In tree with female plus male	1	4	5
		12	23	35
	Other contexts	5	7	12
	Total	42	117	159
Female	No other possums in vicinity	1	3	4
	Den tree (own and other) .	3	5	8
	Adult in vicinity (in all cases a female)	0	5	5
	Joey only following	0	1	1
	Total	4	14	18
Total		46	131	177

Table 4.14

Observations of chinning and chesting+ by the three central males and three central females during the 1966 all-night observation period, tested for independence against sex of marker and site of marking, using the G-test (Sokal and Rohlf 1969, Box 16.9). +Chesting includes observations accompanied by chinning.

A	B	C		
Marking site	Sex of Marker	No. of observations Type of Marking		
		Chinning	Chesting	Total
Ground	Male	8	6	14
	Female	1	1	2
		9	7	16
Tree base	Male	7	76	83
	Female	2	8	10
		9	84	93
In tree	Male	19	29	48
	Female	3	5	8
		22	34	56
Total		40	125	165

Hypothesis tested	d.f.	G	P
A x B independence	2	0.408	>.5
A x C "	2	26.666	<.005+++
B x C "	1	0.396	>.5
A x B x C interaction	2	0.768	>.5
A x B x C independence	7	28.238	<.005+++

Partitioning : site x type of marking

Marking proportions			G (level of significance:2 d.f.)	
Chinning : Chesting			Ground	In tree
.56	: .44	Ground	-	
.39	: .61	In tree	1.448	-
.10	: .90	Tree base	16.618+++	13.208+++

similar to that of the adult males exploring den trees other than their own.

Young males also exhibited marking in response to the spotlight. In one observation Male 6214 stood up on his hind legs and chinned the branch beside him immediately the spotlight was shone onto him. Fifteen minutes later he again chinned the branch when the filtered beam of the spotlight was shone onto him. In another observation the young unmarked male who visited the three den trees reacted to the spotlight beam. He ran about 18m to a tree and chested the base two or three times.

4.2312 Relative Frequency

A summary of the contexts within which adult male and adult female chinning or chesting was observed during the 1966 all-night observations is given in Table 4.13. Because of the regular manner of the observations this summary is indicative of the relative frequency of observation, both in relation to the sex of the marker and of the context. It is apparent that males mark about eight times more frequently than females and that about two thirds of their observed marking was in the absence of another possum. However, as previously discussed, much of the marking in the absence of other possums was at places with a history of prior use by a possum. Of the marking performed by a male in the vicinity of another possum over three quarters was in the vicinity of an oestrous female. This indicates that an oestrous female stimulates male marking, but as mentioned earlier, his marking is not directed at the female. Three quarters of the female marking was performed either at places with a known history of possum use (i.e. den trees) or in the presence of another possum, usually another female or her joey.

A significant dependence occurred between chinning and chesting, and the site at which it was performed, but not with the sex of the marker (Table 4.14). With partitioning it is apparent that the ratio of chesting to chinning at a tree base (9.3:1) was significantly greater than that which occurred either in a tree or on the ground where the ratio was close to 1:1 (Table 4.14).

In the 1966 observations used above it was not possible to separate chinning which actually occurred with chesting. Thus the observations of

chesting also contain an unknown proportion of chinning, which could affect the probability of chinning occurring as treated above. In an attempt to overcome this difficulty observations of male marking made during the 1968 courtship period are used, because observations were made when much closer to the possums and it was easier to distinguish chinning which occurred with chesting (Table 4.15).

Table 4.15

The number of observations of chinning alone, chesting alone, and chesting with chinning performed by adult males during the courtship observation period of Jan.-Apr. 1968, in relation to the site of marking. Tested for independence with the G-test.

Marking Site	Type of marking			
	Chinning alone	Chesting alone	Chinning with Chesting	Total
Ground	1	0	1	2
Tree base	2	18	5	25
In Tree	22	13	12	47
Total	25	31	18	74

$G = 18.718$, 4 d.f. $p < .005^{+++}$

Tree base In tree

$G = 16.450$, 2 d.f. $p < .005^{+++}$

As before there is still a significant dependence between type of marking and site. If we ignore ground marking because of low numbers, there is still a significant difference in the ratios of the type of marking which occurs at a tree base and actually in a tree. From inspection of the data it is apparent that a high proportion of the tree base marking is chesting on its own where as in a tree there is a much higher proportion of chinning, either on its own or accompanying chesting (Table 4.15). When the observations of chesting and chesting accompanied by chinning are combined, as in the 1966 observations, the ratios of chinning to chesting (ground 1:1, in tree 1:1.1, and tree base 1:11.5) are similar to the 1966 ratios.

This difference in site selection for chinning and chesting was one of

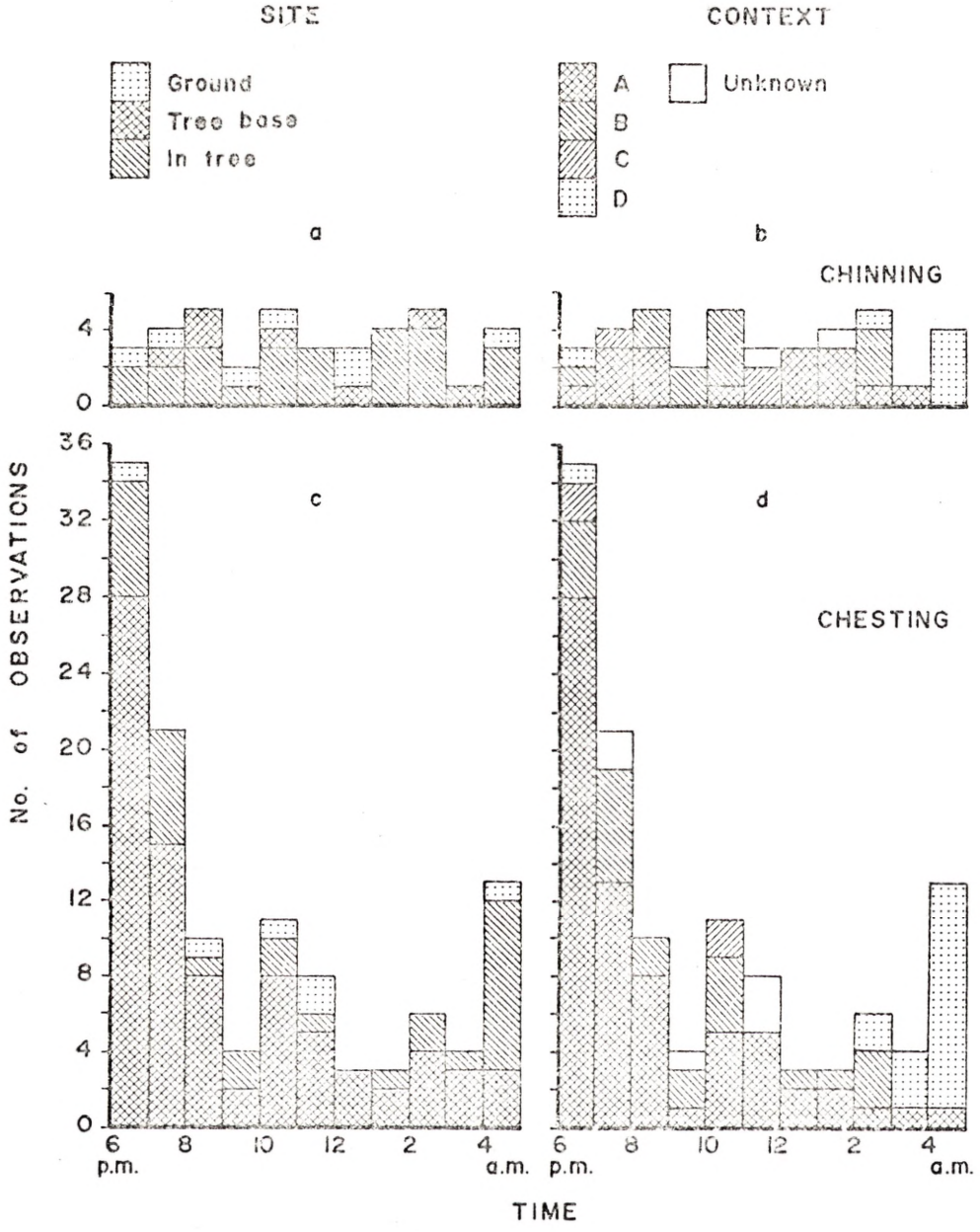


Figure 4.30 : Nightly distribution of chinning and chesting in relation to marking site and context. Contexts - A = no other possum in vicinity, B = oestrous female in vicinity, C = anoestrous female or male in vicinity, D = marking own den tree.

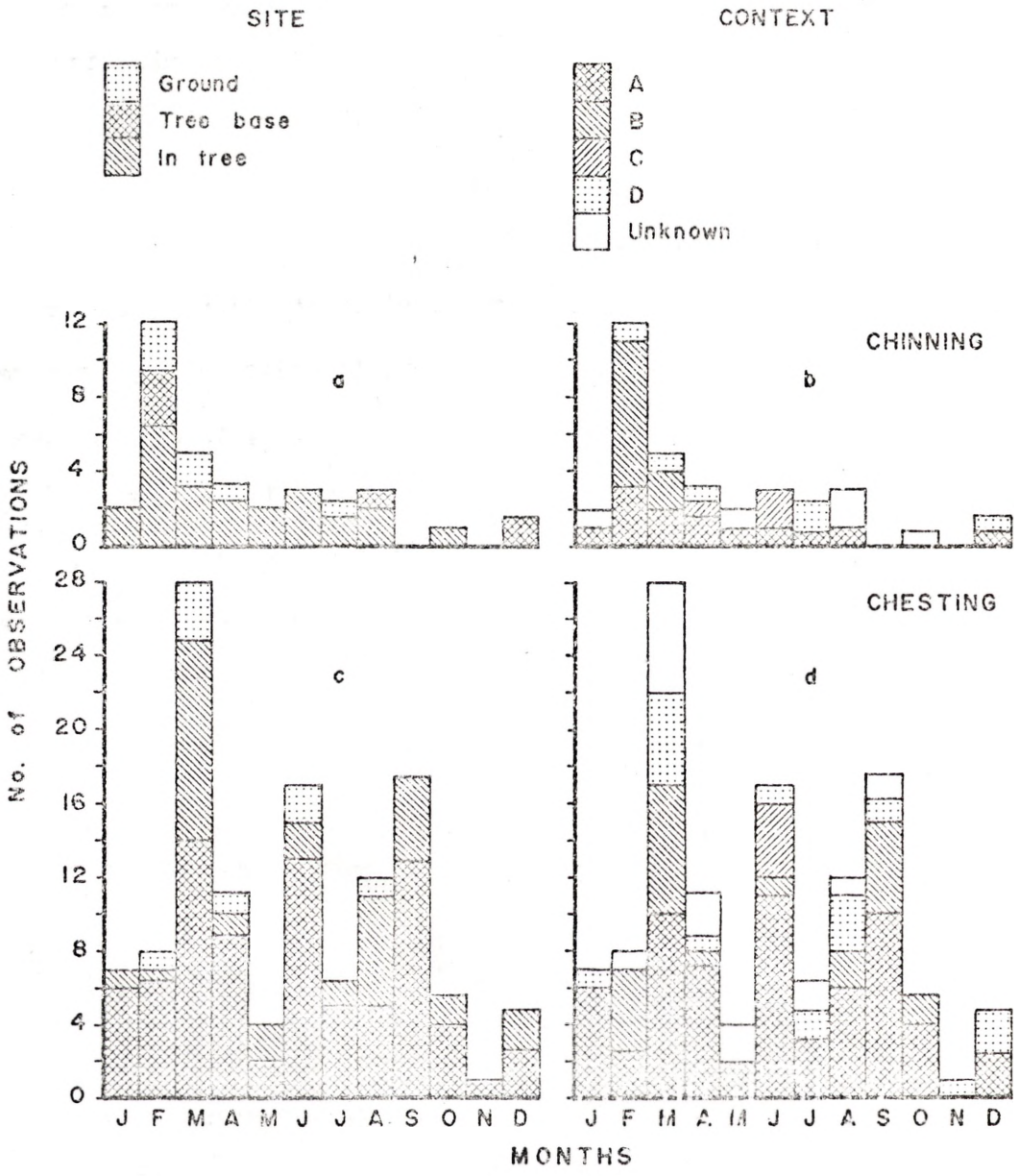


Figure 4.31 : Seasonal distribution of chinning and chesting in relation to marking site and context. Contexts - A = no other possum in vicinity, B = oestrous female in vicinity, C = anoestrous female or male in vicinity, D = marking own den tree.

three differences between the two behaviours detected in the present study. The other two are in the temporal patterns described below. No differences, however, were detected in the contexts in which chinning and chesting were performed, or in responses to the two types of marking.

4.2313 Temporal Pattern

4.23131 Nightly

Only adult males are considered because of insufficient data for females.

Chinning was evenly distributed throughout the night with no apparent separation into either site or context according to time, except for own den marking which was the only form of chinning observed after 4.00 a.m. (Fig. 4.30 a&b

Chesting on the other hand exhibited a marked peak early in the evening which consisted predominantly of tree base marking performed in the absence of other possums (Fig. 4.30 c&d). Most of this marking was done when the males were travelling on the ground after coming down from their den trees. A second smaller peak is evident at dawn consisting almost exclusively of own-den marking when the males returned at dawn, most of this being tree branch marking.

4.23132 Seasonal

Again only males are considered (Fig. 4.31).

Chinning shows a pronounced peak in February, the predominant context being that of an oestrous female in the vicinity. From September to January very little chinning was observed.

Chesting shows a definite peak in March with other peaks in June and September. Very little was observed from October to December. The March and September peaks have a higher proportion of oestrous-female-in-vicinity context than the June peak, and the March peak a higher proportion of marking-own-den then the others.

The March and September peaks of chesting can be correlated with increased sexual activity as indicated by the peaks in conceptions of these two months (see Chapter 3). The June peak was the result of increased marking by Jack and Gus which corresponded to a young female (Jess) in their home ranges coming into oestrous for the first time and giving birth to a joey on

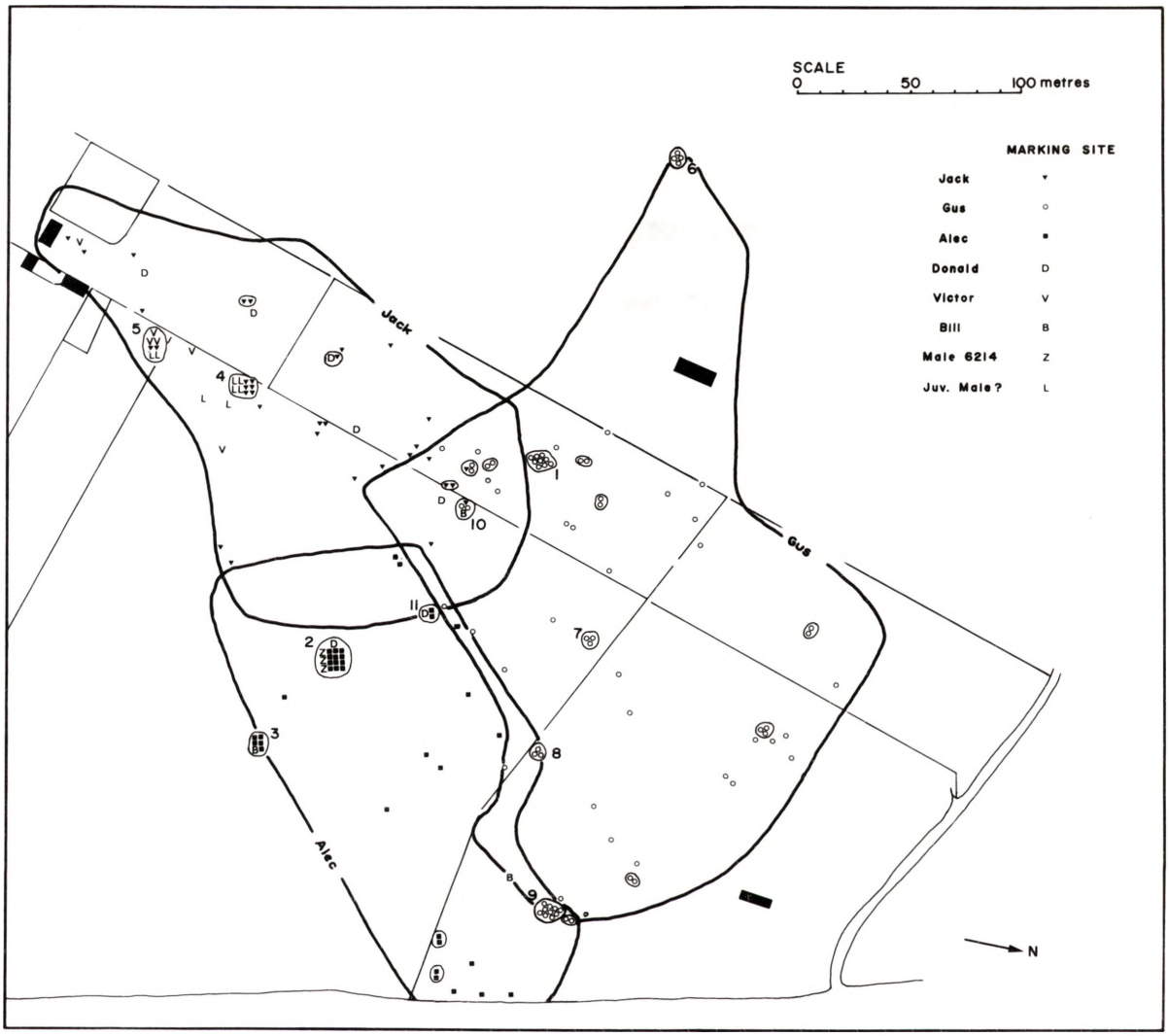


Figure 4.32 : Spatial distribution of chinning and chesting (not separated) by the three central males during 1966. Marking of the same tree circled; numbers are marking foci (see text); heavy lines = home ranges.

the 9th July.

The chinning peak in February is one month earlier than the corresponding chesting peak. This suggests that chinning is the predominant form of marking early in the breeding season - possibly corresponding to the early phases of courtship and that chesting becomes relatively more important later when mating actually occurs.

4.2314 Spatial Distribution

Chinning and chesting by the three central males during 1966 was scattered throughout their home ranges but with definite foci (Fig. 4.32). These foci were mainly dens regularly used or visited by the established male and by other males (Foci 1-7 Fig. 4.32). For example Focus 1 was a large den tree used by Gus and Gert, and Gus was observed marking 9 times over 7 separate nights scattered throughout the year, 6 of the markings when he returned to the tree at dawn. Similarly Focus 2 was a large den tree regularly used by Alec and Alice. It was also used and marked by the young Male 6214, and by Donald who once was observed making an exploratory sally into the area.

Focus 8 was also a den tree but one that was very rarely used. One night Gus climbed into the dead tree and thoroughly sniffed and marked the branches near the den entrance. Very early in the study an unmarked male had climbed into this tree and had examined and marked it in the same way.

Other focal points (Foci 9-11) were not associated with dens. At 9 Gus was observed to mark a large tree 10 times on 2 nights during a period of 3-4 weeks when the tree was being used as a feed tree by Gert, who was in oestrus. The remaining two were trees marked by 2 or 3 males and provided the only evidence that non-den trees may not be marked at random. The tree at focus 10 for instance was marked by Donald on two separate nights, by Jack on another night, and by the juvenile male Bill when he made an exploratory sally into the area. On the other hand Gus frequently passed this tree without stopping to sniff at or mark it.

There was no evidence of boundary marking being performed by the males.

4.2315 Response

An olfactory signal when placed on a substrate may be effective long

after it is deposited. This makes it difficult to know whether a possum is responding to an olfactory signal, and it can only be assumed that it is if it alters its behaviour at the point of marking. This assumption is strengthened if the possum sniffs the substrate, but "sniffing-at" need not be an essential prerequisite to the detection of the scent. It is more likely that "sniffing-at" follows the initial detection, and may be a more careful examination of a scent signal already detected. The absence of "sniffing-at", therefore, does not imply lack of scent detection, but rather a lack of especial interest in any scents detected.

Certain assumptions have to be made in the examination of the response of possums to scent signals. (1) Scent deposited on a substrate i.e. by chinning, chesting, or urine marking, is assumed to have a function life of one night. This assumption is made in the absence of any knowledge of how long the scent does in fact last, except in the case of scent from the secretion of the scent gland which lasted at least 24 hours. (2) A possum was assumed to have detected a scent signal if it came within 0.3m of the substrate marked in the same night, even if the possum did not "sniff-at" the substrate. In most cases the possum passed right over the place marked.

4.23151 Adult male to male (12 obs)

The most common situation was one in which one male marked the base of a tree, and later another male came to the base of the tree (7 obs). In 5 of these the second male also chested the tree base, and in 2 he sniffed at but did not mark the base. In 4 of the observations the first male had climbed the tree after marking it to join an oestrous female, and in all 4 the second male did not climb the tree. This suggests that the second male may have been deterred from climbing the tree by the scent mark. However, in two the first male and the female had already left the tree, and in one the female was staring down at the male on the ground and because she was low in the tree she may have deterred him from climbing. Only in one observation were the first male and the female still in the tree. On this occasion the second male had apparently followed the scent trail of the first

male and female to the tree. On reaching the base of the tree he had sniffed it, peered up into the tree, then stayed within 1m of the base for 1 to 2 min before finally moving away. The male in the tree was known to be dominant to the one on the ground and it was apparently the presence of this dominant male with the female that deterred the second male from climbing the tree.

One of the observations differed markedly from the above. Bill, a young male 21-25 months old had chested the base of a den tree at dawn and then climbed to the den. Ten minutes later Alec, the adult resident male, had approached the tree and chested the base. Alec then climbed the tree at speed, much faster than usual, and immediately ran along the horizontal branch towards the den. Bill, in the meantime, had hurriedly vacated the den. In this case the reaction, presumably to the scent, had been to approach rather than to move away from the marker. It is inferred that Alec was aware that another male had climbed his den tree because such a response was atypical of any shown towards a female. It was not possible to be certain that he had recognised the other male in his tree as the young male living in his area. However, Alec's rapid climbing of the tree suggested that he knew that a subordinate male was in his den tree. Irrespective of the status of the male in the tree the scent mark left by the first male at the base of the tree had not acted as a deterrent. In fact it had the opposite effect and stimulated a rapid approach.

Response, or rather lack of response, to a mark on the branch of a tree was observed only once. Donald and Male 22 had been keeping close to Female 3 who was in oestrus. Donald, the older and dominant male, chested a branch. Within an hour Male 22 passed over the spot but took no notice of it.

A male returning to a place he had previously marked the same night (5 obs), responded once by chesting and once by sniffing. In the first case Donald had chested a small vertical branch as he followed a female. They returned along the branch 1¼ hr later and he chested the

small branch again although the female completely ignored it. In the second Donald had chinned and chested a branch where an oestrous female had been sitting. An hour later he again passed the spot and stopped to sniff but not to mark. With the remaining 3 observations the male had marked the base of a tree and had returned more than an hour later. In none of the 3 did the male show any overt sign that he had detected the scent mark even though he had been within 0.3m of the spot marked.

4.23152 Juvenile Male to Adult Male (4 obs)

Three of the observations occurred when a male climbed into a den tree and thoroughly investigated it. Two were of the young unmarked male who had investigated and marked the three den trees one after the other. In two of the trees an adult male had been present earlier in the night and had performed some marking. However, his behaviour appeared to be orientated to exploring and marking the den trees, rather than a specific response to the marking of the older males. In the third a young male of about 21 months of age had climbed the den tree vacated earlier that night. He very carefully sniffed the branches, paying particular attention to where the two adults had been, but these were not necessarily the places where the adult male had twice chested and once chinned the branches. Again the responsewas more one orientated towards a general investigation of a den tree.

In the fourth observation Gerald (9 months old) passed very close to the base of a tree chested by Jack $\frac{3}{4}$ hr earlier, but he completely ignored the tree.

4.23153 Adult Female to Adult Male (9 obs)

Complete lack of interest was the characteristic response of a female to the scent mark of a male.

In six of the observations the male had marked a branch and the female had then walked along the branch without sniffing or giving any indication that she had detected the scent. In two she did sit on the branch where the male had marked, but both were favourite perches outside

a den.

Twice a female descended a tree, ignoring the base where a male had chested it, and once a female completely ignored the ground within 0.3m of her, where a male had thoroughly chested the ground half an hour previously.

4.23154 Joey to Mother (12 obs)

A joey-at-heel was the only class of individual that came close enough to a female scent mark for a response to be recorded.

On 5 occasions a female chinned or chested a branch as she walked along it, and in 3 of these she also urine marked. Her joey was following 1 to 1½m behind and cautiously watching its mother (who by this time was beginning to behave antoagonistically towards her joey) and appeared to completely ignore the marked branch. Only once did the joey briefly sniff at the place lightly chinned by its mother, then continued to follow her as before.

During Female 6147's exploration of the dead den stump as already described, she chinned or chested the stump 5 times. Her daughter, although she carefully sniffed and once even chinned the den rim, appeared to orientate her behaviour towards an investigation of the den rather than to a response of her mother's scent marking.

On another two occasions Female 6147 marked the base of a tree as she travelled on the ground. Each time her daughter, who was following about 1m behind, completely ignored the tree base.

In general therefore a possum's response to another possum's chinning and chesting appeared minimal. Frequently the mark appeared to be completely ignored. In the case of males there may be a tendency to mark where another male has marked, but apart from that there was little overt positive or negative reaction to a scent. Once a marked tree base may have acted as a deterrent to a following male, and once the mark appeared to stimulate a rapid approach, indicating that the mark itself is neither an innate repellant or attractant.

4.232 Scent Gland Secretion

In the field the liberation of scent gland secretion was never observed, although scent was twice detected. Once at the base of a tree soon after a male, who was following a female and her joey had passed it, and once outside a den. Alltogether 7 dens were examined closely and it was only at one of them that the scent was detected, nor was it ever detected in or around the two dens in the roof of my house.

Possums of either sex liberated the scent gland secretion if they struggled violently while being handled.

Under cage conditions the two males, but not the female, liberated the secretion, and three contexts were recognised. In the first context the adult male and female had been in the cage for about a month when a specimen tube containing scent gland secretion was taped to the upper surface of an horizontal pole. The secretion had been collected 4-5 hours earlier from the cloaca of a male who had released it during a struggle while being handled. The caged male walked over the tube 3 times without taking any notice of it, but stopped the fourth time to sniff at it for about 1½ seconds. He then walked away from the tube and climbed the wire of the cage and hung upside down with his cloaca protruding and wet with the cream coloured scent gland secretion. At the same time he gave slight pelvic thrusts and made quiet clicks, both of which suggest sexual arousal. The female sniffed at the tube once and took no further notice of it, her cloaca remained flat and she did not click. This response of the male is completely different to that observed by Thompson and Pears (1962) which was a typical aggressive response, with the male rearing up into an upright stance with the front paws held ready to strike.

In the second context a second male, Victor, was introduced into the cage several weeks after the first two, and kept in one half separate from the others. Whenever the connecting door between the two halves of the cage was opened, aggressive encounters frequently occurred between the two males. After the first night these encounters were initiated and won by Victor who was obviously the dominant male. Victor's cloaca remained flat during these encounters and he never released any of the scent gland secretion, but the cloaca of the other male was invariably protruding and frequently saturated

with the secretion. Victor showed no apparent response to the strong smell of the secretion coming from the male and it did not appear to deter him from attacking the other male. It must be remembered, however, that these encounters took place in unnaturally confined situations which is likely to distort both the liberation of the scent and the response of Victor to it.

The third context was one in which Victor ran away from me along a horizontal pole, leaving sinuous strips of secretion on the pole when I had startled him by an abrupt entry into the cage. He was the only male in the cage as the other had been released a month earlier.

4.233 Urine Marking

Urine marking was not seen at all during the 1966 all-night observation period, and only 17 observations (9 male, 8 female) were made at other times. In some of these observations urine marking was assumed to have taken place because of the action of lowering the hind quarters or because urine was seen glistening on the cloacal vibrissae.

Six of the 9 male observations occurred when the male was in the same tree as an oestrous female. The other 3 were in the absence of any other possums; once when an unmarked male had explored a den tree he appeared to do some cloacal marking, and twice when a male was travelling through trees by the river's edge frequented by other possums. Victor, when kept in captivity, tended to leave a drip trail when following the oestrous female and at the same time he gave soft courtship calls. No distinction was made between the sigmoid strip and the drip trail in the field, but there is a suggestion from the cage observations that the drip trail is associated with courtship. No response was observed to any male urine mark.

All the female observations were of Female 6147 between the dates 5.12.68 and 21.1.69 at the time when her joey was still following her but she was keeping it at a minimum distance of about 1m. In 4 of these a sigmoid strip was made and in the other 4 the type of mark was not determined. The joey was close behind the female in 4 observations; in one the female urinated at the entrance of a den both were exploring, and in the other two when the joey was close but not following.

The joey only responded once by sniffing at a definite sigmoid strip left by the female on a fallen log, but it continued to follow her without any apparent change in behaviour. In at least 3 of the other observations the joey walked right over where the female had urinated without taking any notice of the urine on the branch.

No female, but some male urine marking was observed during the intensive observations of courtship early in 1968. This suggests that female urine marking increases in frequency, if not being actually restricted to the period when the joey is following its mother.

4.234 Sniffing

Sniffing is an indication that a possum is sampling its olfactory environment, and any subsequent behaviour that can be correlated with the sniffing is inferred to be a response to a scent. The source and type of scent is usually not known but in the present study substrate sniffing, especially in and at the bases of trees was assumed to be in response to scent left by possums.

4.2341 Substrate Sniffing

In continuous bouts of sniffing only the bout, not each sniffing action was recorded. For example a possum walking along a branch may alternate sniffing with looking around, but unless it was interrupted by some other behaviour of sufficient duration or intensity to be recorded in the field notes, the sniffing was recorded as a single observation.

Sniffing was recorded as occurring: (a) on the ground if more than 1m from the base of a tree, (b) at a tree base if the possum climbed no more than 1m then jumped back to the ground, or sniffed the ground within 1m of a tree base, (c) in a tree amongst the branches of a tree, or as the possum climbed the trunk.

Only in the case of a possum sniffing at the exact spot where another possum had been sitting was it possible to be certain about the source of the scent. Otherwise an individual was assumed to be the source of scent if in the same trees as the sniffing possum, or if it had

Table 4.16

Summary of total observations of substrate sniffing at Moggill Farm in relation to site and presumed source of scent. The 1966 all-night observations are in parenthesis.

Sniffer	Source	Site			Total	1966
		Ground	Tree base	In tree		all-night only
Adult Male	Male & Female	1	8	11	20+	8
	Oestrous Female	2	15	79	96	26
	Anoestrous Female	1	4	5	10	9
	Juvenile Female	0	2	16	18	1
	Juvenile Male	0	0	1	1	1
	Adult Male	0	0	8	8	0
	?	13	35	16	64	27
	Total	17(7)	64(14)	137(8)	217	72
Adult Female	Possum	0	3	11	14	8
	?	5	5	10	20	7
	Total	5(1)	8(6)	21(8)	34	15
Juvenile Male		2	2	6	10	
Juvenile Female		1	3	2	6	
Joey		2	1	9	12	
Total		27	78	175	279	

+ 19 oestrous and 1 anoestrous female

(a) Test of independence of source of Total observations x 1966 all-night observations

$G = 18.328$ 8 d.f. $p < .05$+

(b) Test of independence of site of total adult male observations x 1966 all-night observations.

$G = 14.400$ 2 d.f. $p < .005$+++

been observed to traverse previously the same night the spot on the ground being sniffed. When a third individual was present both were assumed to be the source of the scent if both were adults, unless there was clear evidence to the contrary. If the third possum was a joey with its mother, the mother was assumed to be the source of scent with the realisation that this assumption may become progressively less valid with increasing age of the joey.

A summary of substrate sniffing observations in relation to the site and presumed source of scent is given in Table 4.16. However, for a better indication of relative frequencies only the 1966 all-night observations are used even though fewer observations mean more lumping. Although the 1966 observations differ significantly in the relative proportions of sniffing in relation to the source of the scent (Table 4.16), in both series of observations it is apparent that adult males do most of the sniffing and that an oestrous female is the major source of scent investigated by him. This he does at the base of a tree before climbing it to join her, as he climbs the tree, as he follows her along branches, and at places where she had been sitting. This last action was very pronounced, because when a female moved from a branch where she had been sitting the male immediately climbed to where she had been sitting instead of immediately following the female. After carefully sniffing the branch and sometimes marking it he then followed the female. There is also a significant difference in the two series of male observations in relation to the site of sniffing. During the 1966 all-night observations a tree base was the site most frequently recorded, whereas in the total observations most records were of sniffing actually in a tree (Table 4.16). This significant difference is attributed to the intensive courtship observations in early 1968 when observations were made early in the evening when the male and female were still in the female's den tree. Taking the 1966 observations as a truer representation of sniffing sites in general, it follows that tree bases are an important site with regard to the transfer of olfactory information.

Table 4.17

Observations of male substrate sniffing in relation to the presence of another possum in the tree sniffed and whether the male climbed the tree.

Action following sniffing	Another possum		Total
	Absent	Present	
Climbed	3	15+	18
Did not climb	40	6	46
	43	21	64

+ 13 were oestrous females

Test of independence

$G = 25.796$ 1 d.f. $p < .005^{+++}$

(Yate's correction used)

An illustration of the importance of a tree base as a site for olfactory information is the probability of the male climbing the tree after sniffing at its base. The probability is significantly greater ($p < .005$) that he will climb the tree if it contains another possum (usually an oestrous female) (Table 4.17). When the male did not climb a tree containing another possum (6 obs) the other possum was an oestrous female only twice and one of these was with a dominant male. In the remaining four observations the other possum was an anoestrous female twice, and juveniles twice. Where the male climbed an unoccupied tree (3 obs) it was either a den tree (2 obs) or a tree vacated by a female (possibly in oestrous) 1½ hr earlier. These observations suggest that tree base sniffing is a means of checking whether a tree is occupied by another possum. They also suggest that the reproductive status can be determined because of the tendency to climb trees containing an oestrous female.

Much of this tree checking is done when a male is looking for an oestrous female as illustrated in the following protocal:

Protocol: 27.2.66, 20.20 -Gus came down onto the ground and travelled to the N.E. roughly following the route taken by Gert 20 minutes earlier. Although he did not appear to be following a scent trail he was

> obviously following her because when he reached the group of trees where Gert had made a right angle turn he made a similar turn, yet he did not seem certain which tree she had climbed. He sniffed the ground and then jumped onto T1323 and climbed 6 feet up it. He stopped and very carefully sniffed the trunk and peered up into the canopy before jumping back to the ground. Once on the ground he circled round and sniffed the base of T1341 then straight across to T1333, the tree Gert had climbed. He sniffed the base, gave it a quick chin wipe and bounded up without any hesitation.

Occasionally when a male climbed a tree to join a female, he did not go directly up to her but would repeatedly walk out along branches to their end and then back to the trunk, sniffing all the time, and appearing to be searching for her. This searching was rather surprising as one would expect the male to follow the route taken by the female. One explanation may be the way in which a climbing possum will often walk out along a branch, for about 1m, then jump back to the trunk about 0.5m above the crotch. This leaves a gap in the scent trail of the climbing possum which may confuse a following possum.

All male-male sniffing took place in the vicinity of an oestrous female, who was acting as the focus of attraction. The only observations, therefore, in which it was possible to be certain that the male was sniffing at scent left by another male, were of the type in which the sniffing male very carefully examined the place where the other male had either been sitting or been standing for some time (8 obs). Only once did this sniffing lead to a marked change in the behaviour of the sniffing male. On this occasion two fairly evenly matched males (Male 22 and an unmarked male) had one or two encounters in a tree containing an oestrous female, and not long after one of these encounters the unmarked male moved over to where Male 22 had been sitting, and became excited as he sniffed the branches. He then rapidly followed Male 22 who had climbed it a minute or two before. However, when they came face to face both males withdrew. In all the other 7 observations, two of which followed encounters, the sniffing male merely seemed to be carefully checking the scent of the other male, and none resulted in any marked

response.

In the remaining male-male observations it was not possible to say whether the scent originated from the male or the female, but the behaviour of the sniffer sometimes indicated a definite reaction to the presence of the other male. In 9 observations the sniffer reacted by either climbing the tree very slowly, sniffing at it carefully all the time (6 obs), or after sniffing the base rapidly climbed the tree to initiate an encounter with the male already with the female (3 obs). The slow climbers were young males with recently established home ranges of their own. They kept 3 to 6m from the male already with the female and did not initiate any encounters. The fast climbers, on the other hand, were older well established males who in all three cases displaced the male already with the female.

Jack once showed a marked change in behaviour which I attribute to the scent of Donald, who was dominant to Jack. Immediately after coming down from his den tree, Jack rapidly trotted over to Jill's den tree where he sniffed the ground and the base of the tree. He then trotted about in an excited manner in the vicinity of her den tree, sniffing at tree bases and the ground, apparently looking for Jill. She had already come down her den tree and been joined by Donald. Jack picked up their scent trail on the ground and followed it slowly, sniffing carefully and frequently sitting in the upright alert. He followed the scent trail, the only time a possum was ever seen following a trail on the ground, to the tree which Donald and Jill had climbed 20 min earlier. He very carefully sniffed the ground at the base of the tree then sat up on his haunches to peer into the tree, but instead of climbing, which he would almost certainly have done if Jill had been alone, he stayed near the base for 3 to 4 minutes then moved away. The presence of Donald appeared to have deterred him from joining Jill.

The series of adult male-juvenile female observations (18 obs) mainly involved two females (17 obs) who were almost certainly coming into oestrus for the first ime at the age of 12 months. Similarly

5 of the 10 male-anoestrous female observations were with females rather doubtfully classified as anoestrus when they may in fact have been in oestrus.

A high proportion of sniffing by males occurred in situations in which no other possum was directly associated with the scent. These included extended sniffing bouts by males exploring den trees other than their own (3 obs), some sniffing of his own den tree on returning to it at dawn (3 obs), and in trees which had been vacated by females earlier the same night or extensively used by them the previous night. Five of the 13 ground sniffing observations were intensive sniffing with associated chinning and chesting of a confined area.

In comparison to the males, females did very little sniffing. The most characteristic female sniffing situation was one in which she sniffed at the den used by a male. This occurred when a male and a female shared the same den tree, but not the same den. Soon after coming out of her den the female would climb to the den used by the male, usually after he had left it, and very carefully sniff round the entrance and often then enter the den. Sniffing as such was recorded only twice in this investigation of a male's den, but the action of going into his den happened more frequently and it is assumed that sniffing took place. A den box under the eaves of my house was rather infrequently used by the resident adult male, but nearly every time that he did use it the resident female climbed into it and stayed in it for 10 to 15 minutes. Once she even urinated in it. The female appeared to be carefully and methodically checking the presence of the male and at no time did she become excited, nor did it appear to be an attempt to exclude him from the den.

Sometimes a female very carefully sniffed a tree as she climbed it to initiate an agonistic encounter, in which she was the winner. Twice Alice climbed into trees containing young males - her 9 month old son Andy in one instance and the young Male 6214 (her son?) in the other instance - and displaced them from the tree. Each time she climbed the

tree slowly, sniffing at it carefully as she climbed, and the young males hurriedly vacated the trees without her having to chase them. In a third very similar observation Jess carefully sniffed the tree as she climbed up it towards Jill. The two females had a brief scuffle and Jess chased Jill down the small tree. In all three of these examples the sniffing female gave the impression that her sole purpose for climbing the tree was to displace the other possum.

The other contexts within which female sniffing occurred are similar to contexts in which male sniffing occurred. One is the observation of Female 6147, followed by her joey, thoroughly investigating the den stump as already described. This was the same type of exploring carried out by males in den trees not being used by them at the time. A female, like the male, also sniffed very carefully at places where another possum had been sitting, but less frequently. In one Gert sniffed at the branch where Gus had been sitting before he gave way to her. In the other Jill's joey had followed Jack, apparently mistaking him for Jill. When it seemed to realise its mistake the joey climbed into a tree where it was later joined by Jill. When Jill first climbed into the tree she went up to the branch where the joey had been sitting and very carefully sniffed the spot. This seemed to satisfy Jill that she had found her joey because she then started to feed about 10m below the joey.

Observations of sniffing by juveniles and joeys were too few to be able to comment on the contexts, except to note that the youngest possum observed substrate sniffing was 236 days old when it sniffed at a branch traversed by its mother who was travelling ahead of it.

4.2342 Air Sniffing

Air sniffing was rarely recorded and because of the difficulties of determining the sources of the scent these records are ignored.

4.24 Discussion of Olfactory Behaviour

4.241 Introduction

Functionally the deposition of scent on a substrate may act in two ways,

which are not mutually exclusive but which may vary in relative importance. Firstly scent may act as a source of information for the marker by enabling the animal to recognise its own area or by helping it to find its way about. This is included in the concept of familiarity which is frequently given as one of the functions of a home range (Kleiman 1966, Jolly 1966, Ewer 1968a), and in the concept of reassurance behaviour (Ewer 1968a). Secondly scent can act as a source of information for other animals, particularly members of the same species, concerning the animal giving the scent signal. This is included in the concept of territoriality (Mykytowyez 1962, 1965, Lockie 1966, Jolly 1966), and in the more general concept of spatial dispersion of individuals whether territorial or otherwise (e.g. Leyhausen 1965).

The information content of a scent signal deposited on a substrate will vary according to the ability of the receiver to recognise individual, sex, group or species scents. That mammals have this ability has been demonstrated for a number of species (Ralls 1971). Individual recognition has been demonstrated in the Sugar Glider (Schultze-Westrum 1965), dogs (Kalmus 1955), gerbils (Dagg and Windsor 1971), in white-mice which can recognise at least 18 individuals (Kalkoswki 1967), and in nestling rabbits (Mykytowycz and Ward 1971). Recognition of sex, group and species scents have also been demonstrated (Schultze-Westrum 1965, Dagg and Windsor 1971, Muller-Schwarze 1971, Dixon and MacKintosh 1971 and Epple 1971).

In the brush-tail possum the response of males to scent left by chinning and chesting showed a trend (not significant) in which the male marked where another male had chinned or chested (4/7 obs) but ignored his own work (5/6 obs). This suggests that a male can at least distinguish his own scent. Also his responses following olfactory investigation of tree bases suggest that he can distinguish between oestrous and anoestrous females and between young subordinate and older dominant males. His investigation of a place where a female had been sitting suggests that he is checking the sexual phase of the female. That males can distinguish the endocrine state of a female has been demonstrated in rhesus monkeys (Michael and Keverne 1968, Michael, Keverne and Bonsall 1971).

4.242 Chinning and Chesting

A high proportion of chinning and chesting took place in the vicinity of another possum or at places known to have been previously visited by another possum. Even in other contexts it was often possible to show a prior use by a possum of the place marked.

It is argued that marking occurs when a possum is aroused by social or other stimuli. This is particularly noticeable in much of the marking performed by a male in the presence of an oestrous female. A state of arousal is evident when he approaches a female to within the individual distance of 1-1½m, when sitting over her den at dusk waiting for her to come out, when giving way in front of her, or after an encounter with the female when the male may become extremely agitated.

Even in situations where arousal can not be detected by agitation or excitement it is inferred that arousal takes place. A male who marks the base of a tree before climbing it to join a female is coming into the vicinity of the female with an increased probability of agonistic interactions occurring. A den tree is a focal point of possum activity with increased probability of meeting another possum, hence an inferred state of arousal and accompanying marking. Similarly with non den trees having a history of possum use. A female increases the frequency of her marking when the mother-joey bond is breaking down and the mother is beginning to behave aggressively towards her juvenile. It may be significant that marking was only observed by mothers with daughters who, as shown in Chapter 5, compete directly for the maternal den. Tree base marking by males travelling on the ground is mainly done early in the night when the possum appears particularly alert as indicated by frequently sitting in the bipedal alert posture. Later in the night the degree of alertness appears to wane, possibly as the individual habituates to stimuli such as strange noises.

Marking in response to the spotlight beam is an example of an asocial stimulus causing arousal and consequent marking.

Arousal has been associated with olfactory behaviour in other

mammals. For example Schultze-Westrum (1965) was able to stimulate olfactory marking in the marsupial glider Petaurus breviceps papuanus, by placing together the cages containing members of a foreign tribe. Jolly (1966 p.49) has noted that olfactory marking of the lemur, Propithecus v. verreauxi, occurs whenever the animal is excited as in territorial disputes, in sexual behaviour, and probably in dominance behaviour.

A contextual analysis of chinning and chesting suggests that its social function is to advertise the presence of the marker to a possible rival for a limited resource such as a female or a den.

Most marking performed by a male in the vicinity of an oestrous female is at places where another male arriving on the scene is likely to come across the mark i.e. at the tree base, at the female's den, and where the female had been sitting.

A possum returning to its den at dawn marks where any individual coming later will pass the mark i.e. at the base of the tree or on the way up to the den. The exploring and marking of den trees other than their own distributes scent at important focal points.

Tree base marking by a male early in the night distributes his scent in his home range. Since it is not a border type of marking the distribution will be more dense and the marks fresher in areas used most frequently.

Female marking is performed in front of her joey with the probability of the joey passing the mark being high. Thus the mark is apparently directed at the joey at a time when the mother-joey bond is breaking down.

Response of individuals was difficult to determine in the field. Males tended to chin or chest a similar mark left by another male. Often, however, a male ignored a scent mark and this was the typical response of females and juveniles. In a preliminary study of the reaction of both Trichosurus vulpecula and T.caninus to scent, Thompson and Pears (1962) state that the sternal gland exudate elicited only a mild response from both sexes. They do not say what the response was except to imply

that it was not the rearing up into the upright threat posture.

In the present study there was no evidence that the scent per se of the mark acted as a deterent or territorial mark. Rather the evidence suggests that scent marking acts in a more subtle way. It advertises the presence of the marker to other individuals using the area. The response of an individual may then be determined by the age of the mark and the amount of individual information that can be detected from the mark. Assuming individual recognition, then the response will be determined by previous interactions between the individuals in which dominance has been learnt. Similarly the response to tree base marks, distributed generally in another male's home range, may depend on the relative dominance of the individuals. The density and the freshness of the marks will give information on the probability of a face to face interaction and a system of mutual avoidence discussed further in Chapter 6 may operate along similar lines as suggested for domestic cats by Leyhausen (1965).

Association of a scent mark with an agonistic interaction may first be learnt during the breakdown of the mother-joey bond, when female marking is concomitant with aggression directed at her joey. It is this learnt association, possibly reinforced by later interactions when an adult, and not the signal per se which may allow the signal to act as a territorial type mark (see also Kleiman 1966). That a scent signal deposited on a substrate automatically acts as a deterrent in territorial marking has been questioned by Baran and Glickman (1970). They in fact found that gerbils were attracted to objects that had been "territorial marked" by the ventral gland-pad sebum of conspecifics. Similarly Mykytowycz and Hesterman (1970) found that dominant males who are territorial were attracted to strange dung-hills which act as foci for scent marking with faeces. In the present study the observations of chinning and chesting tend to confirm the above observations that the scent actually acts as an attractant and stimulates marking.

Bolliger and Hardy (1944) suggested that the function of the

sternal gland was to attract "...the other sex by its colour and by the odour...", and that a male marks a "....tree or a building which it inhabits in order to guide the prospective partner". Also that the odour, and probably the stain, from the sternal region of the mother may assist the young to find its parent after it has left the pouch because "...in this period the female sternal secretion seems to be at its maximum". It seems unlikely that the odour from the sternal gland acts as an attractant as suggested by Bolliger and Hardy. Male marking is not performed in places where a female is likely to come across it but rather where following males will detect the signal. Also it is males who join females in their den trees and not visa versa (see Chapter 6). The increased marking by a female after her joey has left the pouch occurs when the mother-joey bond is being actively broken by the female, by which time the joey has begun to travel independently and has presumably learnt its way around the maternal home range.

Since chinning and chesting are distinct behaviour patterns with a difference in the type of site marked, associated with glandular areas of similar glands but in different proportions, they probably have different meanings if only one of degree. There is also the possibility that saliva deposited by chinning gives the scent left by chinning an odour distinct from that of the sternal gland. Alternatively the two behaviour patterns may merely be a matter of convenience depending on the position of the possum in relation to the substrate. In other words it may be easier to chest the base of a tree, but easier to chin a branch.

From the evolutionary point of view, increased arousal as a causal factor fits in with the general thesis that scent marking in mammals originated as autonomic responses, such as seating and pilcerection (Morris 1956, Kleiman 1966). Kleiman (loc. cit.) has suggested that the evolution of scent marking as a form of assurance preceded the evolution of its social function. This is so if the assurance value of the scent is interspecific, but the evolution of intraspecific assurance value of scent must of necessity have evolved at the same time as its social

function. Once an animal can distinguish between its own scent and that of conspecifics from the properties of the scent alone, a necessity for intraspecific assurance, the use of scent in communication becomes possible. This may then be followed by the further evolution of the social function through the possibility of recognising individuals, beyond the requirements of a strictly assurance function which requires only that an individual be able to distinguish its own scent from others.

4.243 Scent Gland Secretion

Release of scent gland secretion during times of acute stress has led to the suggestion that the scent is a defence mechanism against predators (Bolliger and Whitten 1948, Thompson and Pears 1962). Kean (1967) points out that there is no evidence for this and states that cats will even eat the gland. However, the domestic cat is not a natural predator. Natural predators such as Eagles, goannas (Troughton 1962), carpet snakes (Ogilvie, pers. comm.) and probably the larger owls, are natural predators. Whether they are deterred from attacking the possum by the odour of the scent gland secretion is not known. It has also been suggested that the scent plays a role in sexual behaviour because of the larger glands in the males and the ability to detect between male and female secretion (Thompson and Pears 1962). Sexual dimorphism, however, does not necessarily mean that it has a direct sexual function. Thirdly it is thought to act as a territorial marker because of the marked reaction of males to the scent (Thompson and Pears 1962).

In the present study possums liberated the scent sometimes when violently struggling while being handled, and also during social interactions, when it was the subordinate possum which released the scent. In both of these contexts the release of scent is apparently indicative of fear, and because of this it is suggested that apart from any anti-preditor function it functions as a socially submissive signal. Although the observations showed no evidence that the scent was an effective inhibitor of attack by the dominant individual, these observations are not conclusive one way or the other because of the cramped artificial

conditions under which they were made.

The observations by Thompson and Pears (1962) in which a male rears up into the upright threat posture when presented with the scent gland secretion of another male, appears to contradict the suggestion that the scent is a submissive signal. This may not, in fact, be a contradiction because most serious male-male fights start with a head on rush without any preliminary aggressive display. Therefore the rearing up into the upright threat posture represents the possible change of a head on rush attack into a threat posture, which is partial inhibition.

Several properties of the scent are in accord with this suggested function as a submissive signal. The secretion is only released at specific times not continuously. When it is released it is in copious amounts. It is the strongest scent (to human observers) produced by the possum and will therefore mask any others when it is released. This ensures its detection particularly in situations of considerable tension. Thirdly it is produced when the possums are close together which is essential for a quick acting olfactory signal (Bossert and Wilson 1963). One property which is inconsistant with this idea is the persistance of the scent for days after it becomes smeared on a branch. One would expect a rapid fade of the signal. However, the possum may be able to recognise the freshly released scent from the older scent.

Obviously this hypothesis that the scent gland secretion is a submissive signal needs rigorous testing, which was beyond the scope of this study. A similar function for scent has been suggested to occur in other mammals. The marsupial glider, Petaurus breviceps papuanus, has a pair of anal glands homologous to the scent glands in Trichosurus which secrete a white oil secretion strongly smelling of musk (Schultze-Westrum 1965). The secretion is released when an individual rolls onto its back into a clearly submissive posture, but Schultze-Westrum was unable to demonstrate any deterrent effect of the actual scent. Mice (Mus musculus) have been shown to have a "fear" scent released in social interactions, (Ropartz 1968), and the urine of females inhibits male

aggression (Dixon & MacKintosh 1971).

4.244 Urine Marking

Little urine marking was observed in the present study and the only contextual association detected was that female urine marking occurred when the mother-joey bond was breaking down.

With the special behaviours of depositing urine either as a sigmoid strip or a drip trail there seems little doubt, however, that it has a social function. Kean (1967) considers the function to be "...associated with proprietory rights recognised by a marking possum..." because in a cage situation urine marking was deposited on some but not all horizontal poles available to an individual. He also suggests that the cells from the anal cell glands give an added persistance to odour of deposited urine. Bolliger & Whitten (1948) found that cells from the cell gland were particularly numerous in immature animals and that in adults the cells are more numerous in the urine of males. Often it was difficult to find them in the urine of an adult female.

The only response to urine was for another individual to briefly sniff at it. The amount of information obtained from the urine odour is not known, but if cells from the cell gland contribute to the odour then at least age and sex of an individual may be determined.

4.245 Sniffing

Substrate sniffing was the most common form observed, and a very high proportion was at places where another possum was either known or inferred to have been. Substrate sniffing therefore was socially orientated.

Males sniffing in situations involving an oestrous female were the most common observations. Two functions of this male sniffing are apparent. Firstly a male may locate a female by scent and the sniffing of tree bases is an example of this as indicated by the significantly higher probability of a male climbing a tree containing a female after he had sniffed at its base. Searching may also have been the function of much of the tree branch sniffing as a male climbed a tree. Secondly

male sniffing may be to detect the onset of oestrus. Most obviously coming into this category is the careful sniffing of a branch where a female had been sitting for any length of time. When sitting on a branch a possum's cloaca comes into contact with the branch, thus depositing any secretions from the cloacal area onto the branch. The cellular composition of the vaginal smear changes during the oestrous cycle (Pilton and Sharman 1962), and a copious vaginal mucous secreted 3 to 4 days prior to ovulation saturates the fur in the cloacal region (Hughes and Rodger 1971). It is quite probable therefore that the male can detect the time to mate from these secretions. He sniffs at scent left on a branch rather than at the female's cloaca, because until the female is ready to actually mate she prevents the male from approaching within about 0.5m (Chapter 5).

Males were also observed to sniff carefully at points where other males had been sitting. Vaginal secretions are therefore not the only source of scent left on a branch. Faeces, urine and secretions from the paracloacal glands may all contribute to a scent spectrum which is particularly strong at places where a possum has been sitting.

Kean (1967) observed that caged males followed lactating females and suggested that the glands lining the pouch may be the source of a scent attractant. At Moggill Farm males also showed an interest in a lactating female but only at the stage when a joey had left the pouch. This interest corresponded to a minor spring peak of mating when the females presumably come into oestrus again, and oestrus may be the result of a reduction or cessation of lactation (see Pilton and Sharman 1962 and Sharman 1962).

4.246 Concluding Remarks

That olfactory communication is important to the brush-tail possum is indicated by the number of glands and associated behaviours to do with scent marking and scent release, a summary of which is given in Table 4.13.

Table 4.18

Summary of olfactory communication of *Trichosurus vulpecula*

Gland	Behaviour	Done by+	Possible message	Possible meaning	Response from others
Sebaceous, chin	chinning	♂ ♀	identity and emotional state of individual	location and status state of individual	chinning or chesting approach or withdrawal depending on relative status
Sebaceous, chest	chesting	♂ ♀			
Holocrine, cloacal	urine dribbling	♂ ♀			none apparent
Apocrine, cloacal	emmission	♂ ♀	fear	submission?	inhibition of aggression?

+ underlining denotes main performer

It is assumed that each set of glands associated with olfactory communication conveys a different message, otherwise there is little selective advantage in developing more than one set of glands. In the present study it has been possible to distinguish only between the message conveyed by the paracloacal scent glands and the rest. Fear is apparently the scent message conveyed by the scent glands and there is some slight evidence that this may act as an inhibitor of aggression in conspecifics. The sebaceous chin and chest glands, and probably urine as well apparently all convey the message of location of an individual and possibly information regarding the individuals status. However, no difference in the message of these latter three could be detected.

The closely related Sugar Glider (*Petaurus breviceps papuanus*) has a number of glands and associated marking behaviours, and Schultze-Westrum (1965) has been able to demonstrate different functions falling into species,

tribe and individual scents. A more detailed examination of the brush-tail possum may demonstrate similar categories of scent. The most significant difference between these two marsupials is the complete lack of bodily contact scent marking between individual possums, an indication that the possum is a more solitary species than the sugar Glider.

VISUAL COMMUNICATION

The importance of visual communication to a nocturnal mammal is difficult to asses in a field study. Jones (1921) contended that vision was not well developed in the possum on the basis of a blind individual being collected in otherwise excellent physical condition. On the other hand, Trichosurus vulpecula has a spherical eyeball which is an adaptation to night vision (Walls 1963). In the present study possums appeared to "watch" each other when both in the same tree, or when one was peering down at another one on the ground below. It is possible that the "watching" possums were in fact listening to the other possum as it moved about, but this seems unlikely because on a clear starlight night even a human observer can pick up the blurred outlines of a possum particularly when silhouetted against the sky. Also possums will leap from one branch to another which is indicative of vision being used.

Kean (1967) correlates ear positions of the possum with emotions such as fear, anger etc. and states that in one position the lighter backs of the ears are visible fromin front implying a visual communicative function. Also he maintains that the "light upper surface of the paws is displayed" during a threat posture, again implying a communicative function. Bolliger and Hardy (1944) suggest that the colour of the sternal gland as well as its scent has a communicative function. However, neither Kean nor Bolliger and Hardy critically examined ear position or colour patterns in relation to visual communication, and so their observations are at the speculative level. Nevertheless colour patches such as the sternal gland have been demonstrated to have a visual function in the golden hamster where an increase in flight behaviour was observed in males paired with males in which the black ventral mark had been intensified by dyeing (Grant, MacKintosh and Lerwill 1970). The general colour of the brush-tail possum is dark grey dorsally and on the flanks,

with a lighter colour, usually an off white, ventrally which gives a distinct contrast to the dorsal colour. In the most intense type of threat a possum rears up on its hind legs with front paws held ready to strike (Chapter 5), and the light coloured belly is exposed. There seems little doubt that the lighter colour would be seen by the other possum in the interaction, and the darker streak of the sternal gland may also be visible and thus function as a visual signal as suggested by Bolliger and Hardy (1944). Apart from the marked contrast between the dorsal and ventral colouring of a possum it seems doubtful that smaller colour patches with less contrast such as the backs of ears and paws are used as visual signals. However, this needs to be examined critically.

CHAPTER 5

SOCIAL RELATIONSHIPS

The interpretation of social relationships of the possum is predominantly based on the interactions between two individuals because when more than two possums were involved the group acted as a loose aggregate, with only rarely any suggestion of a group acting as a cohesive social unit.

Before proceeding with the discussion of relationships, definitions and descriptions of the types of interactions and relevant motor patterns are given below.

5.1 DEFINITION AND DESCRIPTION OF AGONISTIC BEHAVIOURS

5.11 Approach

An approach is the movement of one possum towards another leading to a social interaction, irrespective of whether the approaching possum is aware of the other possum. Usually approach was obviously synonymous with initiate, but approach is used in preference because it avoided having to make decisions as to whether the approaching possum was the one who actually initiated the interaction. A Relaxed Approach was by either walking in the normal relaxed manner or by climbing at the normal speed. Usually the approacher looked directly at the other possum and had its ears swivelled forward to point directly at the other. Sometimes, however, the approacher sniffed the substrate during the approach. A Rapid Approach included trotting, running, bounding and rapid climbing. It also included an approach where one possum jumped across from one branch to the branch of the other possum. On the ground the rapid approach was characteristically a bound, whereas in a tree it was a run along a branch, occasionally by a jump from one branch to another or by a rapid ascent or descent of the trunk. A distinct form was the Low Rush in which the approaching possum ran along the branch, but over the last metre or two lowered the body much closer to the branch by flexing the elbows, and with head thrust forward rushed at the other possum. A Deliberate Approach was a slow yet very deliberate walk with the head slightly lowered and thrust forward as the approacher gazed intently at the other possum. It gave the

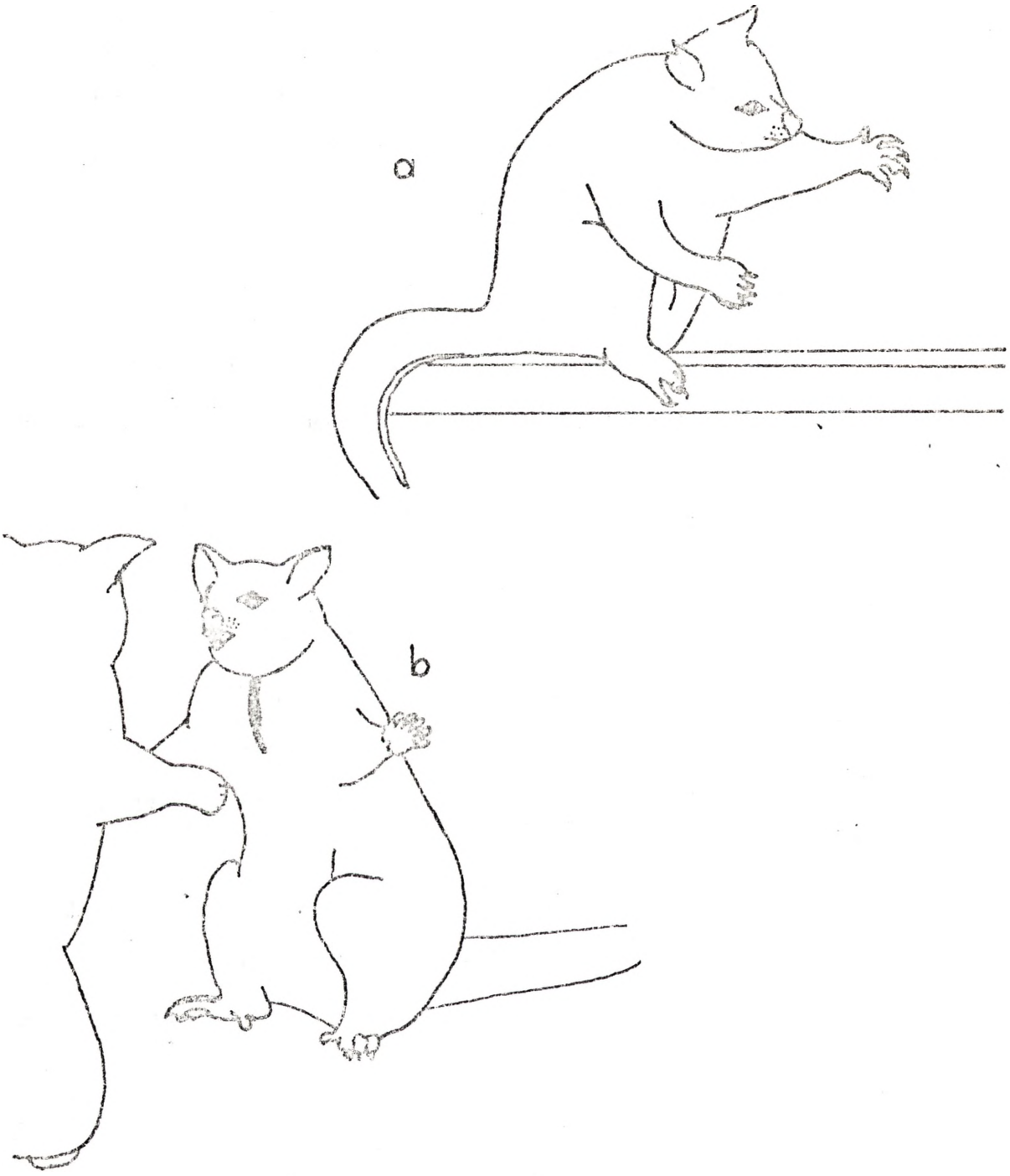


Figure 5.1 : Raised paw threat. a) low intensity, b) high intensity. Traced from photographs in Ridpath (1967 p 36, 37).

impression of a tense controlled approach in which the possum appeared to be about to dash forward. A Cautious Approach was one in which the approacher paused when within 2m of the other, then continued the approach very slowly, with clear signs of ambivalence between approach and withdrawal. The body tended to be pressed closely to the branch and the forward movement tended to be by small erratic movements.

5.12 Withdrawal

An interaction was terminated by one possum moving away from the other either by walking or climbing at a relaxed pace - relaxed withdrawal - or by running, bounding, jumping or some other equivalent mode of locomotion - rapid withdrawal.

5.13 Raised Paw Threat

A series of postures indicating a possum's readiness to strike at another were considered threatening. In the least intense form a possum merely lifted one front paw off the substrate but with increased intensity the paw was raised higher and quickly became distinguishable from the raised paw alert in which the paw hung relaxed, then both front paws were raised and the threatening possum sat more and more upright on its hind legs, until in the most intense form it was bolt upright in the bipedal posture with its front paws out to each side at shoulder height ready to strike (Fig. 5.1). The impression gained was that the hand was held open with the fingers extended but in at least one photograph the fingers remained curled.

When no attack followed the raised paw threat the possum dropped back to all fours, sometimes keeping one fore paw slightly raised. If an attack did follow, it was usually in the form of a forward lunge, varying from a slight forward lunge with a rapid downward strike of the paw, usually just one, but sometimes a rapidly repeated series of three or four strikes not necessarily all making contact. From the bolt upright bipedal threat the most intense form of attack was a bipedal leap which brought the attacker down on top of the other possum and which is described more fully in 'rolling and leaping' fights. When a possum rears up into a bipedal posture it exposes its lighter coloured underparts, and it is this by which the other possum may recognise

that a threat is occurring.

5.14 Nose-to-nose

Occasionally on meeting, two possums stretched their noses towards each other with the rhinaria 3-4cm though sometimes up to about 30cm apart. The rhinaria did not appear to touch, except possibly in some mother-joey interactions, and presumably the two possums were sniffing at each other, because a tame possum was heard to make snuffling sounds when in a similar position. Some tactile communication may be involved because the whiskers can be turned forward to extend about 2cm beyond the tip of the nose.

5.15 Intense Stare

An intense stare was recognised as such when a possum remained motionless with its head thrust forward slightly as it gazed directly at another possum. Sometimes the stare was accentuated by a slight lowering of the neck and head below the level of the shoulders. The intense stare was often associated with the deliberate approach.

5.16 Agonistic Interactions

Agonistic interactions are those in which attack, threat or fleeing behaviour is apparent (see Hinde 1970 p.336 for definition), and although sexual behaviour may be implicit in such interactions it is not overtly expressed.

Agonistic interactions were the most common type of interaction between possums and therefore are described in detail below. However, any features which appear to be sex or age dependent are considered in the latter section on relationships.

Three main types of agonistic interaction were recognised, the give-way, chase and fight in a progressively more aggressive series, with numerous subdivisions also recognised.

Interactions were short, usually with clearly defined beginnings and endings, but in any one interaction little attempt is made to split it into the main components of give-way, chase and fight, all of which may be present. Rather the interaction is classified according to the most aggressive component present. Unless otherwise stated therefore a chase leading into a fight would

be classified as a fight.

In some cases it was necessary to distinguish between a pause contained within a relatively long interaction, and two separate interactions occurring very close together. If during the break both possums switched to some other activity such as feeding, grooming or sitting then the first interaction was considered to have terminated, and to have been followed by a second interaction. If on the other hand, only one possum changed its activity but the other continued to stare at its opponent, then the break was considered to be a pause in a single interaction.

5.161 Give-way Interactions

A give-way interaction was one in which a possum approached another and one of them turned aside or moved aside in apparent response to the other, without there being a fight or a chase.

It was necessary to clearly define the distinction between a give-way and a chase. A give-way became a chase only if both possums moved rapidly, one following the other, and then only if the following possum showed definite signs that it was reacting to the possum in front. For example a possum rapidly descending a tree, with the apparent intention of leaving the tree, might disturb a second possum lower in the tree who then also rapidly descended the tree ahead of the first. This would be classified as a give-way, not a chase, because of the following possum's apparent lack of positive reaction to the other. In practice it was relatively easy to distinguish between a rapid give-way and a chase.

For descriptive purposes give-ways can be conveniently subdivided according to the movements of the participants relative to one another. Several types of give-way interactions were recognised but no precise definition of them is attempted as they represent modes in a continuum. Description of typical give-way interactions are given below as an indication of the range of interactions that can occur.

Type 1 This was typically a male-female interaction with the male making a relaxed approach along a branch towards a female. When within about 1m of the female he paused, possibly because of threatening behaviour from her

Figure 5.2 : Approach and withdrawal sequence typical of Type 1 give-way interaction. a) Male approaches female who has one front paw raised off branch, b) male turns as female gives raised-paw threat, c) female watches male withdraw, one paw still raised.

in the form of a raised paw or a hiss as she sat and watched him. He then turned and withdrew, his turning sometimes coinciding with an increase in the intensity of the female's threat. His withdrawal was usually relaxed. Once about 2-3m from the female he would usually turn to face the female again. The female usually sat throughout the male's approach and withdrawal, but occasionally she moved to meet him, and sometimes followed him when he was withdrawing. The latter sometimes developed into a chase particularly if the male's withdrawal was rapid. Figure 5.2 illustrates a typical sequence in which the male approaches, the female threatens, and he withdraws.

Type 2 was similar to type 1 in that the approacher gave way but there were subtle differences in the behaviour of the approaching possum. Rather than the very relaxed approach of type 1 the approach was more cautious, with ambivalent overtones, with a rapid withdrawal usually coming after the two possums had stared at each other for 10-15 seconds. It was more typically a male-male or female-female interaction lacking the sexual overtones apparent in type 1.

Type 3 The apparent intention of the approaching possum was to pass the other rather than to initiate an interaction. A give-way was considered to have occurred. If in a tree the approacher crossed to a parallel branch when within 2-3m of the other - or rather laboriously clambered through a series of smaller branches as it circled round, or over the possum, keeping 1-2m away. If on a trunk, the approacher moved round to the opposite side, usually increasing its speed of climbing for 1-2m as it actually passed the other possum. The reaction of the approached possum varied, from merely watching, to a lunge in the approacher's direction.

On the ground the approacher veered off at a tangent, or if moving parallel but in the opposite direction, increased its speed from a walk to a trot or a bound for 2-3m, just as it came level with the other in order to "hurry" past. The distance at which the give-way took place tended to be greater than in a tree, and was in the region of 3-6m, and some may have occurred at even greater distances.

Type 4 is a supplanting give-way in which it is the approached possum

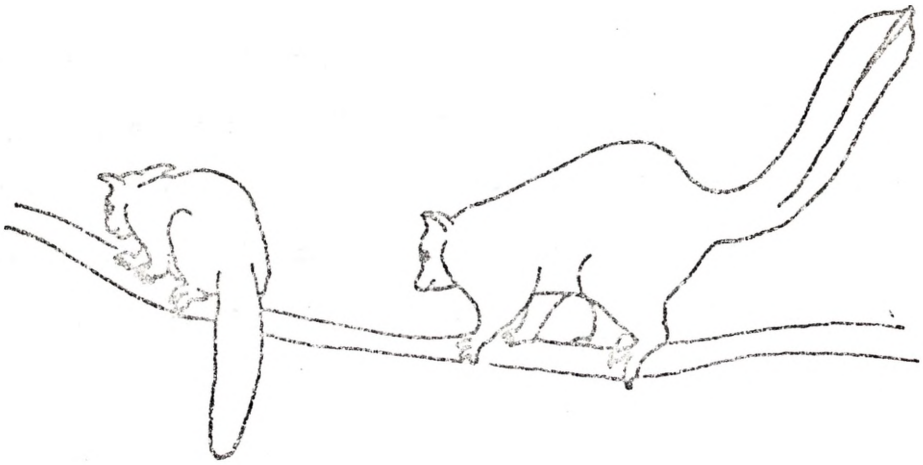


Figure 5.3 : Female approaches male from behind in a supplanting interaction typical of Type 4 give-way. Traced from photograph.

who gives way and the approaching possum stopped at the point where the approached possum had been prior to giving-way. Most observations were of interactions between males and females, with the female being the approacher. Most of her approaches were relaxed, but many had overtones of being deliberate with her head held low and thrust forward. The male usually waited until the female was within 1m before giving way with a relaxed withdrawal. If he delayed longer his withdrawal tended to be rapid. A male was not observed giving a raised paw threat and only very occasionally gave a screech. If he had his back to the female he often crouched low on the branch with ears depressed before withdrawing (Fig. 5.3). There was no indication that the perch itself was the goal of the approaching possum.

Type 5 Similar to type 4 and also typically a female approaching a male, but in this case the female continued to follow the male. She sometimes continued to follow steadily and surely for several metres, most clearly recognised when she continued to follow him until he was on the ground, or on the last 1-2m of the trunk when she stopped. Again this was apparently a displacement interaction, but with a greater displacement factor than the previous type.

Type 6 It was the approached possum who gave way, but in this type the approaching possum was apparently not initiating an interaction. It most commonly occurred when a possum climbed into or left a tree, either climbed higher, or moved down the trunk ahead of the other. Typically the possum giving way began to do so when the other was still 5-6m away i.e. at a much greater distance than in most other types of give-way.

On the ground a possum sometimes jumped onto the base of a tree to look at an approaching possum, then jumped down again and moved away when the other was 5 or more metres away.

Type 7 "The dash-past" (36 obs) This was a very distinct type of give-way which occurred when a possum wished to get past another possum on the same branch or one very close to it. It usually occurred when one possum was cornered at the end of a branch, or at the top of a tree by the other possum. Irrespective of which possum made the initial approach, the one doing the

dashing past broke into a run when about 1m separated them. As they drew level the cornered possum veered slightly but noticeably to one side, thus bring it alongside the other possum, and clearly distinguishing the rapid approach from one which led to a head on encounter and a fight. In extreme cases, as the cornered possum scrambled past, it swung right under the branch and ran "sloth-like" under the other possum. Usually a dash-past led to a brief scuffle but on thicker branches or when passing "sloth-like" a contact interaction was sometimes avoided.

5.162 Chase

A chase was an encounter in which both possums were moving rapidly, one following the other, and in which the following possum showed definite signs that it was reacting to the one in front. Possible confusion between a chase and a rapid give-way encounter has already been discussed under give-way encounters. Chases where classified according to whether they occurred in a tree or on the ground, and whether they were short or long.

5.1621 Tree chase

A tree chase was defined as one in which the chasing possum remained in the tree. This also included chases in which the chasing possum came right down the tree and actually onto the ground, but stopped at the base of the tree and did not move more than 1m away from the tree. Typically a tree chase was preceded by a relaxed approach which brought one possum to within about 2m of another. Only then did one, either the approacher or the approachee run at the other and the chase proper start. In a few chases the final rapid approach of the chasing possum was longer than 2m, but none were preceded by the more determined low rush approach. A few approaches, on the other hand, were deliberate. Frequently the chased possum had begun to give way before the other possum broke into its chasing run.

The length of a tree chase ranged from about 1m to the full height of the tallest tree - i.e. about 25m. Within this range they did tend to fall into two natural groups, but with no sharp distinction between them. A short tree chase (60 obs) was one in which the chasing possum stopped at, or very close to the place where the other possum had been before the chase took place.

If the chaser went beyond this point it appeared as though the momentum of the initial rush caused it to overshoot. Once the chased possum had moved away, the chasing possum appeared to be uninterested in following, i.e. in maintaining the chase. Thus the short chase tended to be restricted to one branch of the tree, or if on the trunk to be shorter than 3m. Functionally therefore it was a supplanting interaction similar to give-way type 4.

A long tree chase (55 obs), on the other hand, was one in which the chasing possum continued with the chase after the initial rush, and was not therefore usually restricted to one branch of the tree or was appreciably longer than 3m. Typically, the possum being chased headed down the tree with the other following 1-2m behind, although this varied from about 3m separating the possums, to chases in which the chasing possum's nose was level with the base of the tail of the one in front. Termination of the chase characteristically occurred near the base of the tree with the lower possum in the head down position about 2m from the ground, and the other possum 1-5m higher and also in the head down position. After a pause the lower possum nearly always jumped to the ground and moved away from the tree at a relaxed pace. The higher possum stayed in the tree, turning to climb back onto a branch as soon as the other had jumped to the ground. Occasionally it followed the other possum onto the ground, but not as a continuation of the chase.

Four main variations of the long chase occurred. First, the chased possum sometimes came right down the tree, and without pausing jumped to the ground and bounded away from the tree. The chasing possum usually stopped on the tree trunk 2-3m off the ground and watched it bound away. Occasionally it also came right down onto the ground but stopped within 1m of the base of the tree. Secondly, seven long tree chases were continued as ground chases. Thirdly, a few chases terminated relatively high in the tree i.e. above the lowest branch, and neither possum left the tree. Fourthly, if at the start of the chase the possum being chased was above, and sometimes when level with the other possum, then the chase tended to go up the tree to the top where, if possible, the chased possum made a wide loop through the canopy before coming down the tree.

A screech was the most common vocalisation associated with the chase and occurred in about ½ of them. It was given either immediately before the chase began or during the actual chase. Other vocalisations were the grunt, usually accompanying a screech, and the chatter (brief or short) which tended to be given by the winner at the end of the chase.

5.1622 Ground chase

A ground chase was one which took place entirely on the ground, although a few started on the base of a tree within 2m of the ground.

Several types were recognised.

Short ground chase This was the most common type observed with 14 occurring alone and another 5 either preceded or followed by a fight. Like the short tree chase, there was a tendency for the chasing possum to make an initial dash at the other possum, and then to stop at, or close to the place where the other had been before the chase. However, in the ground chase the distance separating the two possums when the chaser made its final rapid approach was of the order of 3-5m rather than the 1-2m of the short tree chase. Similarly the chase itself tended to be longer, but usually well within the 20m which was taken to be the arbitrary distance dividing a short ground chase from a long ground chase.

Irrespective of which possum made the initial approach, the actual chase was started by the chaser suddenly bounding towards the other possum. The other then bounded away, often at right angles. Rather than make a right angled turn the chasing possum tended to stop at, or slightly over-shoot the spot where the other possum had been. When moving directly away from the chaser the chased possum sometimes suddenly turned just before stopping so that it was broadside to the one behind, presumably to keep an eye on the chasing possum. Typically the chase terminated by both possums apparently stopping simultaneously 4-5m apart, then one or both walked away without the other following.

Interrupted ground chase A series of short chases sometimes followed one after the other separated by distinct pauses in which one or both possums stood perfectly still, intently gazing towards the other (5 obs). In four of the

observations only two short chases occurred in the series, but the fifth consisted of three and is described in the protocol below.

5.3.66 21.55 Alec on the ground at the base of Mt8 watched Bill (a juvenile male) approach and when he was 4-5 yds away Alec made a dash at him. Bill darted to one side and Alec shot past him, then turned and stopped. After a pause Alec again chased Bill for about 5-10 yds. before they both stopped. Another brief pause and Alec again chased Bill, this time for 20 yds. and they finished near the base of T718. The only vocalization was a brief chatter at the end of the second chase. Alec began to feed and looked in my direction. Meanwhile Bill passed 5-6 yds. behind Alec who took no apparent notice of him.

A modification of the interrupted chase was one in which the chased possum made sudden changes of direction, sometimes even doubling back on its tracks (3 obs). In one case the chased possum doubled back once and the chaser did not turn to continue the chase, but in the other two several changes of direction occurred and the chasing possum continued to follow. These last two were also interrupted by pauses as in the following protocol where the ground chase started as a tree chase.

3.6.66 01.50 Female 3 chased Gerald down T213 and continued to chase him on the ground. Twice he doubled back in his tracks and the second time she stopped. Gerald also stopped and about 5 yds. from her. They both stood perfectly still, then after about ½ min. Female 3 suddenly chased Gerald again. This time Gerald kept going although she stopped after a few yds. A brief growl was given in both chases.

Long ground chase (6 obs) This was a chase which was noticeably longer than 20m with the longest being more than 200m, but the others were of the order of 30 to 60m. The most characteristic feature of the chase was the persistance of the chasing possum.

Another noticeable feature was the behaviour of the possum being chased. In two of the observations the chased possum ran at full speed in a straight line without the slightest deviation to the side. Both were chases in which one adult female had chased another adult female down a den tree and the chased possum appeared to be leaving the vicinity of the tree as quickly as possible, with the chaser following also at full speed. In another three observations the chased possum tended to travel in a wide circle at a steady lope so that the chase finished very close to where it had started and in one

case the chased possum went back up the tree out of which it had been chased. In another the chased possum twisted and turned instead of travelling in a simple circle, but without any of the sudden changes of direction of the interrupted chase. All three involved adult males in the vicinity of an oestrous female. The sixth and longest chase - over 200m - observed was an intermediate between the circling and the very straight chase. This followed a fight and a long tree chase between two adult males in a tree with a female. The chased possum turned through about 45° every 20-30m, first one side, then the other, to follow a zig zag course, but without the very abrupt changes of an interrupted ground chase. Both males travelled at a steady rather unhurried lope, with the chasing possum apparently not trying to catch the one in front.

Vocalizations during ground chases were similar to those given during tree chases, with the screech being the most common but given in less than a quarter of the chases (6/36 obs). Grunts and chatters were also heard at much the same times as for the tree chases.

The longest ground chase emphasised a feature of chases in general which was not satisfactorily resolved. This was the apparent reluctance in many of the chases of the chasing possum to actually catch the one in front, even when it appeared that it could easily do so. Four aspects of the chases suggested this. First, in a high proportion of chases, possibly as many as half of the tree chases, the chased possum had begun to give way before the other broke into the run of the chase proper. In many cases the give way was rapid and I gained the distinct impression that it was the rapid withdrawal which stimulated the other possum to chase the possum who was withdrawing not visa versa. Secondly, during the actual chase the chasing possum appeared to hang back and deliberately avoid catching up with the one in front, or if it did draw level with the rump of the chased possum it refrained from biting or hitting at it. Thirdly, I gained the distinct but unsubstantiated impression that frequently at the end of the chase, when both possums appeared to stop simultaneously, that it was in fact the one in front who stopped first and the other a fraction of a second later. Fourthly, although the final approach of the chasing possum was often very rapid this was only for the

last metre or so. None of the chases were preceded by the more determined low rush approach which invariably led to a fight. Of course some chases did start without the chased possum turning to give way first, some did terminate by the chaser stopping first, and in some when the possum in front stopped the one behind kept moving and caught up with the former. Finally 16 out of 127 chases terminated in a fight, thus indicating that in at least some instances the level of aggression of the chasing possum was relatively high.

5.163 Fight

A fight is an agonistic encounter in which the participants come into bodily contact with each other, no matter how brief the contact.

Several types were recognised.

Wrestle fight (15 obs) Two possums faced each other and fought by biting at their opponent's head and shoulders, at the same time holding each other's shoulders with their fore paws. The main aim appeared to be to hold each other as they bit one another but tufts of fur were sometimes pulled out and scratches inflicted by the front paws.

Typically the approach was rapid (10/14 obs) with at least four being of the low rush type and no pause occurring so that the possums clashed head on, with the approached possum usually crouching to meet the attacker. Even when the approach was relaxed (4 obs) the approaching possum did not pause but walked straight up to the other and started the fight. All four of these were of a male approaching an oestrous female, who sometimes adopted a raised paw threat posture, but without effect.

Frequently the fighting possums toppled sideways from the branch, but usually managed to cling to the branch with their tails and hind feet, and continued the fight hanging upside down. Only once did two males fall from their branch to a lower one and then to the ground about 3m below, and they remained locked together until hitting the ground.

Termination of the fight was by one possum breaking away and running along the branch, sometimes being chased by the winner.

The longest wrestle took place between two adult males and lasted about

½mn, but was broken into two or three segments by pauses during which the males crouched watching each other.

There was a tendency for wrestle fights between adult males to be relatively quiet with perhaps a short screech at the beginning and one or two grunts during the fight. On the other hand, male-female fights were sometimes comparatively noisy with vigorous screeching, grunting, and growling continuing throughout the fight. This was taken to indicate that the male-male fights were more serious with the participants more intent on biting than on vocalizing.

Two examples of wrestle fights are given in the following protocols.

7.9.66 19.44 Jack has just crossed into T1177. Don ran rapidly up the branch and they met head-on and began to wrestle. They fell from the branch but managed to hold onto it with their tails and hind feet and continued the fight. There was a long drawn out screech when they first met, but after that the only vocalization was one or two quiet grunts as they wrestled. Finally Jack broke away and ran down the branch with Don chasing him. Jack paused but continued as soon as Don caught up with him and he went right down to the ground. Don stopped in the lowest fork about 3m off the ground.

27.2.66 02.43 Gus approached Gert from in front. As he came up to her she raised a front paw in threat, but he did not pause in his approach and walked right up to her. A fight followed accompanied by screeches. They toppled from the branch but clung to it with tails and hind feet as they continued to grapple. Gus broke away and went down the tree 3m to a lower branch. He twitched his tail and gave a growl.

Rump fight (14 obs) A fight in which the attacking possum bit and hit with its front paws at the rump of the other possum. With one exception, the possum being attacked was trying to escape, hence the orientation of the attack. In the exception the attacked possum appeared to be totally unaware of the other's approach from behind.

Considerable variations of the fight occurred. In some the attacking possum hung onto the rump of the other with its teeth and paws, as the attacked possum tried to pull away. In others the fight took place during a chase with the chasing possum striking at the rump of the one in front without a pause in the chase and sometimes the hitting was accompanied by biting at the base of the other's tail.

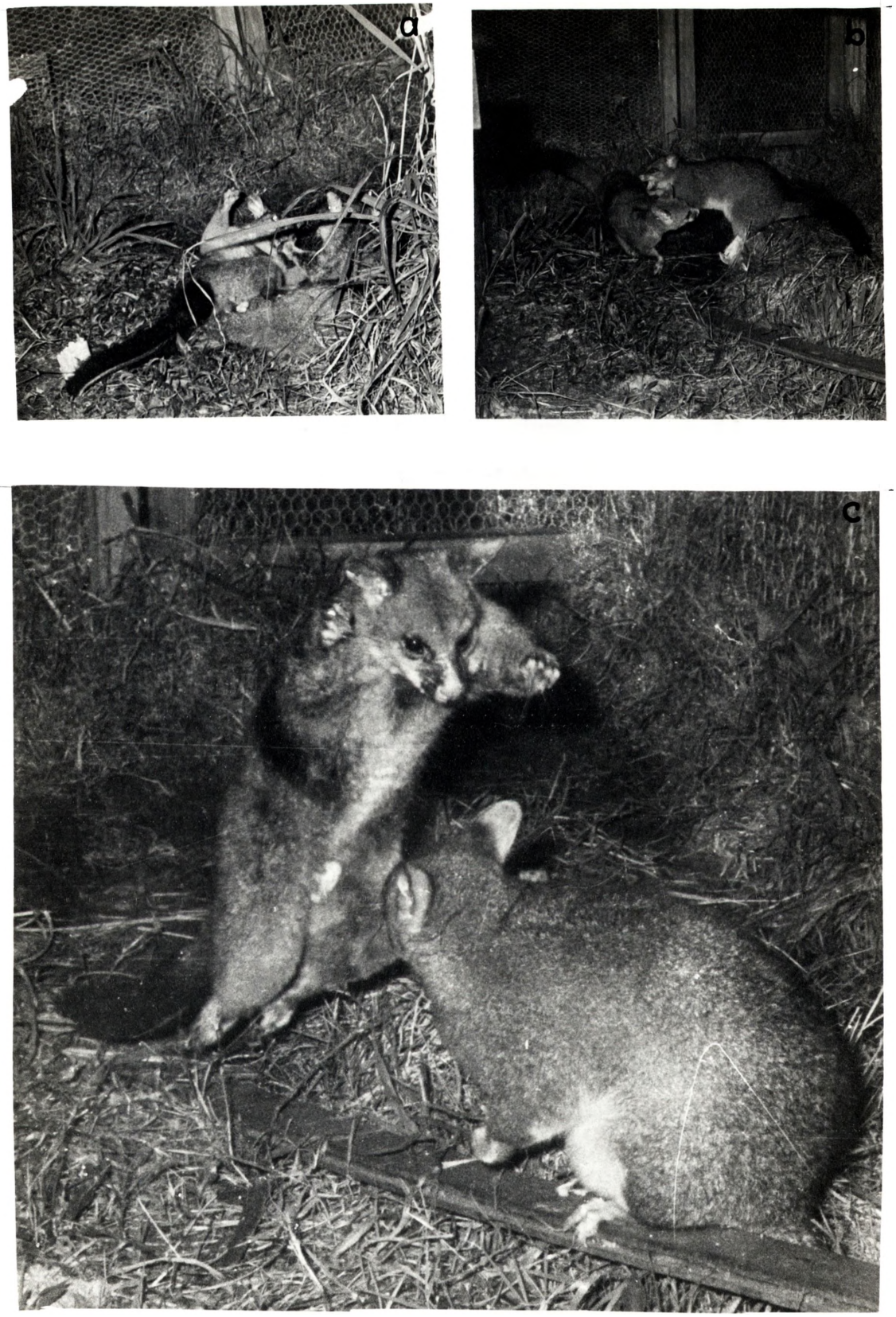


Figure 5.4 : Rolling and leaping fight. a) two males lying on the ground with hindquarters locked together, and raised paw threats, b) preliminary skirmish between male and female, c) male makes a bipedal leap at a crouched female.

Occasionally when caught by the rump the attacked possum twisted round to lash out at its attacker (4/14 obs), but usually there was no such retaliation.

Half of the fights (8/14 obs) were preceded by a chase and one by a dash-past, and in most of the others the attacked possum had turned to move away before being caught. Similarly half (7/14 obs) were followed by a chase, five of these having also been preceded by a chase.

Although accompanied by screeches (3 obs), grunts (1), and chatters (1), the growl (3 obs) appeared to be the most characteristic vocalization of this type of fight. This was because the rump fight was the only time that the growl was recognised as occurring alone, and in an observation at Tyne St. the female gave a very distinct growl as she bit at the base of her juvenile's tail after she had chased the juvenile out of the den.

Rolling and leaping fight (11 obs) A fight characterised by the possums rolling and/or leaping during the fight. They took place on the ground although some started as a chase in a tree and one started as a fight on a netting fence.

In a fight between two apparently evenly matched possums on the ground both tended to roll onto their sides almost as soon as the fight had started. On their sides they lay facing each other either head to head, or head to tail as they bit and struck with their front paws at each other. The hind legs were used only to fend off the other possum, not to deliver vigorous kicks.

Frequently the fight was interrupted by pauses. When lying on their sides both possums stopped biting and clawing at each other and lay facing each other with their head and shoulders propped off the ground by a fore leg and with the other front paw sometimes raised in threat. Their hind legs were usually still pressed against the other and sometimes the tail was wrapped round the other possum (Fig. 5.4). At times one possum stopped fighting, but the other continued to bite at its opponent as in the fight between Jill and Gert (Protocol 27.12.65). These pauses allowed one or other of the possums to get up and move away, and was the only type of fight that was ever observed being terminated other than by one breaking away and rapidly retreating.

Where the participants appeared unevenly matched the attacking possum

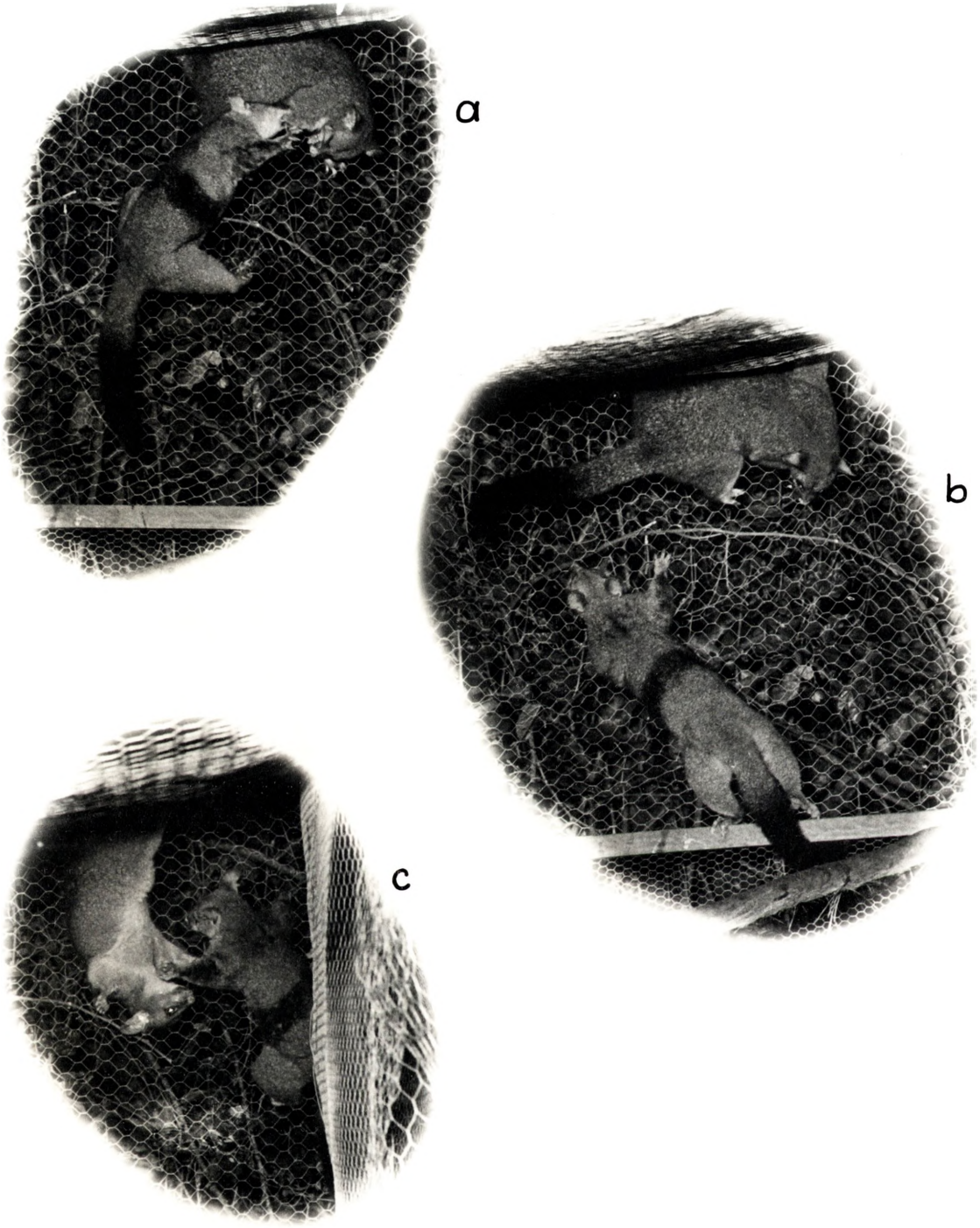


Figure 5.5 : Two males fighting a) biting, b) approach by attacking male (dyed girth), c) raised paw threatening.

rushed at the other and bowled it over as the latter tried to escape. The lower immediately got to its feet and dashed away.

Leaping was another characteristic pattern in these fights. Some fights started by one possum rearing up into the bolt upright raised paw threat posture. It then leapt at the other possum in a bipedal leap during which it maintained its upright posture (Fig. 5.4). When, as in the figure, the other possum was crouched on the ground the leaping possum came down on top of the former's head and shoulders. When, on the other hand, both possums were in the bipedal posture events followed rapidly and it was not observed exactly what happened. Usually ½-1m separated the possums prior to one making a bipedal leap at the other, but on one occasion the distance was greater and could not be covered on one leap. Instead the attacking possum progressed towards the other in a series of two to three bipedal hops, maintaining its upright stance throughout, before landing on its opponent.

Leaping, possibly of a slightly different kind to the above, occurred during a fight when one or both possums would suddenly spring into the air. The body tended to be held vertically as in the above leaps, but I could not determine whether the leaps were evasive or attacking. At least once the leaping possum lashed out with a front paw as it came down.

Rolling and leaping fights were often interrupted by pauses, and a high proportion (9/11 obs) were accompanied by chases either before, during, or after the fight. These chases tended to be short with the participants stopping to stare at each other at the end of the chase. In one fight which involved several chases the role of the chaser and the chased was reversed at least once.

The fights therefore tended to be much longer than any other type but even so only one lasted more than 4 min. and it lasted 15 min. The longest fight was typical because it took place on a 2m high wire mesh fence, but it did have features such as jumping, pauses and short chases which are characteristic of this type of fight. It demonstrates how the basic fighting elements can be varied to suit conditions. Similar fights occurred between captive males on the wire netting of their cage (Fig. 5.5). In the cage fighting

males frequently fell to the ground where they remained locked together on their sides facing each other but lying quite still until one got up.

In the longest fight (described in detail in male-male interactions later) one male kept turning his head down and to one side as he approached the other, thus presenting the back of his head to the other male. This movement is potentially a submissive gesture but did not function as such in the fight. The only other time that head turning was observed was when a mother and her joey had to push past a kookaburra to enter their den. Both turned their heads so that the back of the head was directed towards the long sharp bill of the bird.

Rolling and leaping fights tended to be relatively silent, three were accompanied by a short screech and two by short chatters. Only in the longest fight was it accompanied by almost continuous screeching.

An example of a typical rolling and leaping fight is given in the following protocol.

27.12.65 22.40 Jill and Gert were sitting 10 ft. apart in separate low trees. After about 5-10 mins. Jill came slowly down her tree then suddenly jumped across to Gert's tree and chased her rapidly down to the ground. Jill dashed after Gert on the ground and caught her. A scuffle followed with Jill lying on her side and Gert also on her side, hanging onto Jill's hind leg with her teeth. Gert worried Jill's leg while Jill merely lay on her side with one fore paw raised and watched, making no attempt to tackle Gert. Gert broke away and moved back 2-3 ft. and Jill got up. Gert then rose into bipedal threat, Jill remained on all fours, and while still upright Gert leapt at Jill. She maintained her upright position while in mid air. Another fight followed, shorter than the first, and again Gert broke away and stopped 6 ft. from Jill who did not follow her. Gert looked back and Jill then slowly moved to the north east. Jill took no further notice of Gert but turned and moved back to the base of the tree they had descended.

Worry fight (7 obs) The most prominant feature was that one possum held another with its teeth and worried it by shaking its head from side to side.

Six of the fights observed occurred in a very specific context, one in which one male pulled another male off a female's back with whom the second male was attempting to mate. The unmounted male approached the mounted male and without climbing onto either the female or the mounted male, the unmounted male grasped the other male's back, shoulders, or nape with his teeth. He then proceeded to pull and worry at the mounted male. In all six observations

Figure 5.6 : Sparring fight. Traced from photograph.

the reaction of the mounted male was not to fight the attacking male, but to cling tightly to the female's back with his chin flattened between her shoulders. Usually the worrying male maintained his original grip, but on one occasion he changed it several times, but still confined it to the shoulder and neck region.

In four of the fights the attacking male appeared to actually pull the mounted male off the female's back, and in another, the mounted male suddenly gave a typical screech - apparently in pain - and hurriedly scrambled off the female's back. This last fight was the only one in which any vocalization occurred, the others being silent except for a chatter given at the end of a chase after a fight.

Once dislodged, the mounted male was chased down the tree in three of the encounters, but in the other three the attacking male immediately mounted the female himself and took no further notice of the dislodged male.

One worry fight was observed in a different context to those described above, but neither the participants nor the complete context were known. In it one possum (an adult) was biting and worrying the back of another (a juvenile), and one of them was 'screaming', presumably the one being bitten. Eventually the 'juvenile' broke away and ran rapidly down the branch.

Worrying was also seen during rolling and jumping fights, but it only comprised a minor part of the fight.

Sparring fight (3 obs) Two possums faced each other, both in a low intensity bipedal threat posture (Fig. 5.6). One or both then hit out at the other with a fore paw as they remained in the bipedal postures, and neither bit nor held onto the other although in one fight some fur was dislodged. The blows tended to be very light and the general desultory manner of the fight indicated a low level of aggression. All three were accompanied by screeches and grunts and one was followed by a chase.

Scuffle fight (25 obs) A brief fight which involved biting and/or hitting, but lacked any of the characteristics of the previously described fights.

Brevity was the most consistent feature of the scuffle, sometimes to the point where it was difficult to decide whether or not a fight had taken place.

The only other fight with comparable brevity was the rump fight which was distinguished from the scuffle by its orientation.

Fur was dislodged in some scuffles, but they tended to lack the very characteristic holding action of a wrestle. Undoubtedly, however, some scuffles were abreviated wrestles.

The approach before the scuffle tended to be rapid (14/20 obs), but only two of these were of the low rush type. In most of the others the approaching possum did not break into a run until within 1m of the other possum and was thus virtually a lunge. Two other scuffles were preceded by either a chase or a dash past. Only in three observations was the entire approach relaxed and in two the approacher appeared unaware of the other possum. The only example of a completely relaxed approach preceding a scuffle occurred when Don walked up to Eve without a pause. This was followed a little later by Don mounting Eve indicating he was sexually attracted to her.

A scuffle was terminated by one possum breaking away and usually running down the branch, and in a third of the fights a chase followed the fight.

Vocalizations accompanying the scuffle were common, the most frequent being some sort of screech either just before or during the scuffle (13/25 obs). Grunts sometimes occurred with the screeches, but only twice was a only grunt given. Three scuffles were followed by short chatters, and in one a growl-cum-chatter was given.

The scuffle therefore was a short low intensity fight.

Den fights (5 obs) Fights took place in dens usually accompanied by loud screeches, and/or grunts. In all five fights one of the possums shot out of the den followed by the other who stopped either just inside the den entrance or after a short chase outside the den.

5.2 ADULT MALE - FEMALE RELATIONSHIPS

5.21 Sexual Relationships

5.211 Consort Behaviour

5.2111 Male Behaviour

Mating was often preceded by persistent following of the female by

the male, here referred to as consort behaviour.

The first indication that a female had become sexually attractive was that a male joined her soon after emerging from his den at dusk, which was in marked contrast to his behaviour at other times when he spent some time in his own den tree before moving to another to feed. He immediately crossed to the female's tree, often at a trot and without stopping to feed, and climbed it, frequently arriving before she had emerged from her den, whereupon he stayed close to the entrance and occasionally entered it.

The following observations of Victor's courtship of Female Dim-right-eye are typical. I saw him approach and climb her tree on 5 occasions. Each time he reached the base of her tree within 6 minutes of the first possum to emerge for the night, and once he had begun to climb the tree before it was dark, which was unusually early for a possum to have emerged. His den was within 30m of the female's den tree.

On arriving at Female Dim-right-eye's den tree Victor usually sniffed the ground at the base of the tree, then chinned and chested the tree before beginning to climb. Sometimes he remained at the base of the tree, but never for more than two minutes, sniffing the ground, moving about and sometimes chin or chest marking. His first courtship shook-shock call of the evening was given as he jumped onto the trunk to climb the tree, never before, but sometimes later. As he climbed slowly, Victor sniffed the tree carefully, most attention being paid to a set of low branches, the branch leading up to the den, and the rim of the den entrance.

Victor always arrived at Female Dim-right-eye's den before she had emerged on the five times that he climbed the tree, and twice when he had used a den in the same tree. He sat over the den entrance which opened at the end of a diagonal branch, and leant over to peer into the den. Three nights he climbed right into the den but not far into it because the tip of his tail could always be seen. Once he was chased out by the female, but on other nights he emerged from the den to sit over the entrance again.

In one instance the meeting was not in the female's den tree but in an adjacent tree. The male anticipated the female's route, which always

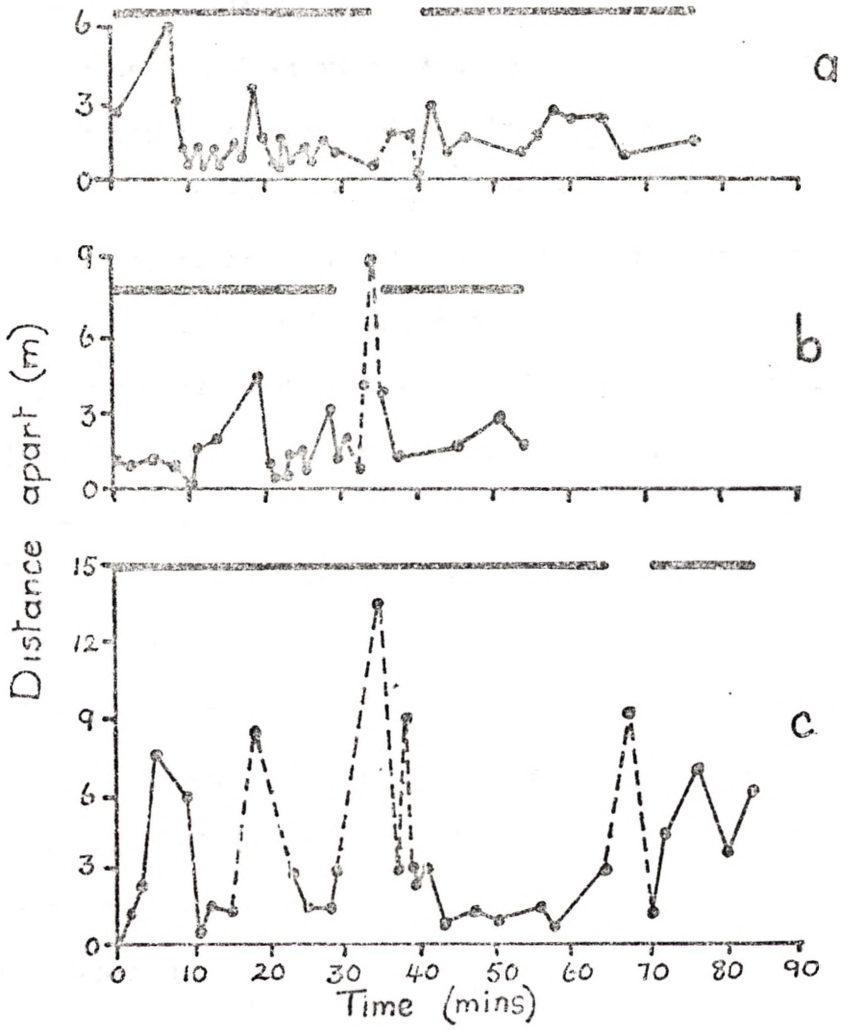


Figure 5.7 : Distance between members of a consort pair (Victor and Female Dim-right-eye) for the first 90 min after the female had emerged from her den. Heavy horizontal line = female in a tree, dashed line = male on the ground.

passed through several trees before coming down to the ground, and waited for her for up to half an hour at a gap which could only be crossed one way.

Males did not always go direct to a female but sometimes appeared to be searching for the female. This was especially so for males not resident in the female's home range, or if the female changed her route. For instance, the first time that Male 33 was seen to penetrate Eve's home range was four nights before she mated. For 0.75 hrs he trotted from tree to tree in the vicinity of Eve's den tree, sniffing at their bases and the ground nearby, sometimes chinned and chested them, and a few times began to climb the tree, usually to jump down to the ground again except once when he climbed to a branch 3m up where he sat for a short while before coming down. Finally he climbed Eve's den tree to the den, but she had left the tree before he arrived and had spent a short time in one of the trees visited by him. Most of the time he moved at a steady trot and did not stop to feed. However once he had visited Eve's den the tempo of his behaviour quietened down as though he had given up looking for her. In another example Male 32 apparently failed to find Alice because she headed in the opposite direction to the one usually taken once on the ground. He climbed into the tree contiguous with her den tree which she had just vacated, then he came down to the ground crossed to and chested the tree she usually went to. Once in the tree his interest in trying to find her appeared to wane and he remained in the tree.

Searching behaviour by the male was also seen when he joined a female in a tree. When apparently not sure of the female's whereabouts in the tree the male walked out to the end of successively higher branches, sniffing along them carefully until he reached her. Having joined the female the male then stayed with her for the greater part of the night. He was the one that maintained the pair by persistently following the female. Rarely did the female follow the male and when she did it usually appeared to be coincidental.

The male tended to keep within 3m of the female when following her. Figure 5.7a plots the distances between the pairs as recorded for a typical

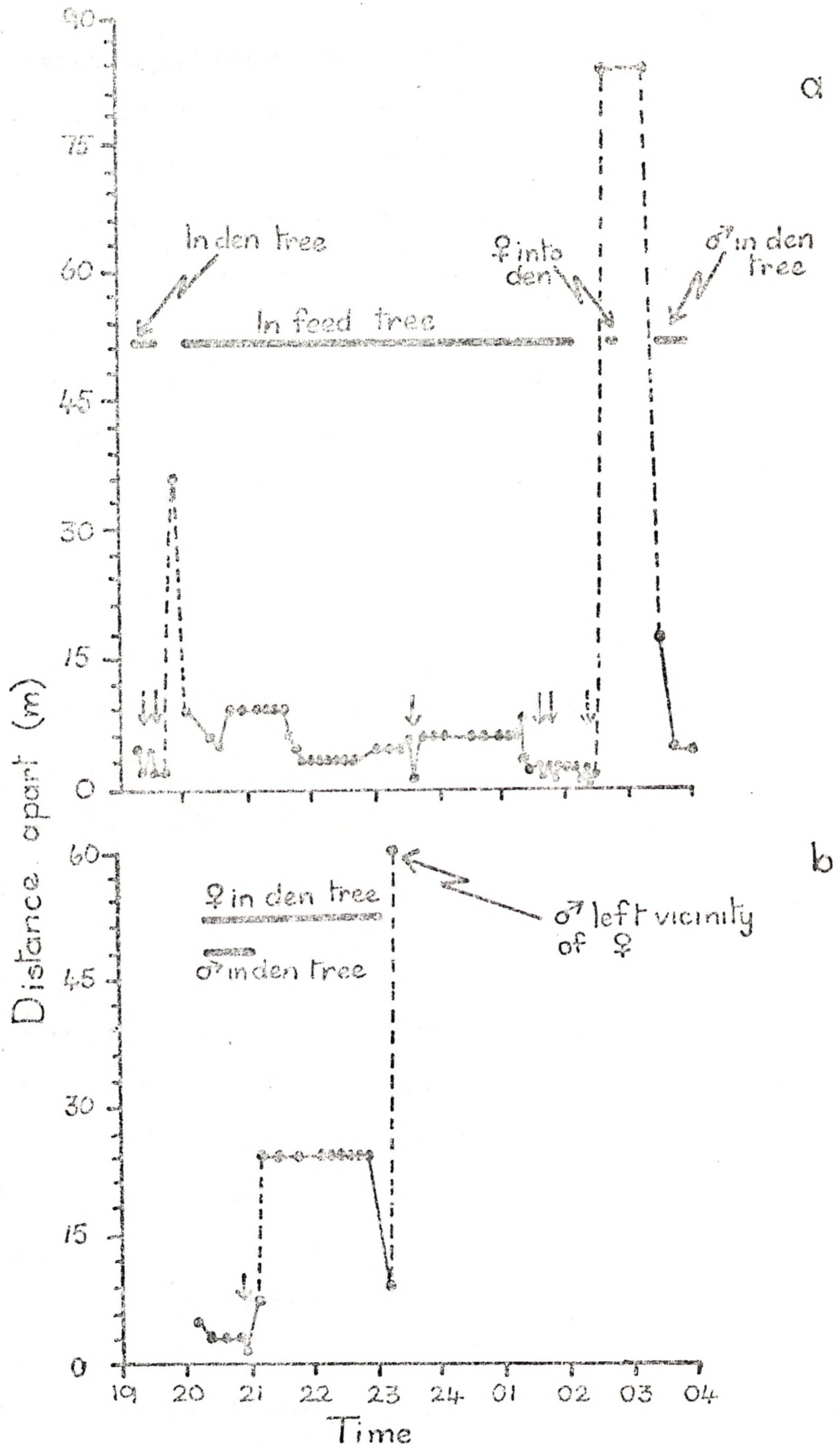


Figure 5.8 : Distance throughout the night between Gus and Gert who shared a den tree.
a) When Gus behaving as consort male.
b) When not behaving as consort male.
Solid arrow = agonistic interaction, broken arrow = attempted mounting by male.

consort pair but because of the method of field recording emphasis was on how close the male came to the female, and not the exact distance between them at all times. A similar trend is apparent in Figure 5.7b except when on the ground the male did move about 9m from the female. In Figure 5.7c the male kept moving away from the female then coming back to her. The first peak at 5 min. occurred when the female moved away from her den and the male, instead of following her immediately, crossed to the den entrance and sniffed around it carefully. The next three peaks at 18, 35, 37 min. were the result of excursions by the male on the ground from the base of the tree, while the female sat on a branch 3m up the tree. When the female did come down onto the ground at 64 min. he followed 2 to 9m behind and on climbing a second tree his interest in the female waned slightly as indicated by the greater distance between them and the fact that he began feeding. A waning of interest by the male in the female after the first hour or two was fairly typical and tended to coincide with the start of the first period of intense feeding for the night.

The male may follow the female throughout the night as shown in Figure 5.8a. The male and female emerged from separate dens in the same den tree and soon afterwards travelled to another tree about 200m distant, where they spent most of the night. When travelling on the ground the male dropped 30 to 40m behind her. Most of the time was spent in the tree feeding and resting with the male keeping 3 to 9m from the female, except for two give-way interactions in which the approaching female came within 1m of the male. On returning to the ground the male followed the female for a few minutes, but then left her and moved to another part of his home range where he fed for nearly an hour. The female headed straight back to her den, and the male returned 1.5 hrs later without taking any further notice of the female.

No systematic attempt was made to record the distance between a male and female when not acting as a consort pair, but Figure 5.8b shows the lack of any close relationship. It was the same pair as in Figure 5.8a with male and female coming out of separate dens in the same den tree. The

male, who was kept under observation all night, left the tree about 0.75 hrs after emerging from his den, but the female stayed in the tree. Apart from one chase which was an avoidance interaction, the male ignored the female and they both went separate ways during the night.

5.2112 Consort Interactions

During the consort period the male's movements were generally concerned in maintaining a relatively constant distance between himself and the female, particularly when this was less than 3m. He did this by following the female, moving and stopping when she did, but often with a time lag, so that the distance was not rigidly maintained throughout. Although obviously interacting with the female, interactions as defined at the beginning of this section were relatively rare.

Most interactions were give-ways. For instance in a typical consort relationship between Victor and Female Dim-right-eye which was closely observed for a total of 7.5 hrs spread over 7 nights in 1968, a total of 31 interactions were observed (mean 4.1/hr, maximum on any one night = 8/hr), and all except one chase were give-way interactions. Half of the give-way interactions (14/30) were typical type 1 in which Victor made the initial approach. He was obviously interested in the female and his approaches were an attempt to come closer to her. Frequently he gave the appeasement shook-shook call as he approached. In the other give-ways (16/30) it was the female who made the approach. Most were of the type in which she appeared disinterested in the male who happened to be on her route. Some however were of type 4 in which the female supplanted the male, and occurred more frequently when she had just emerged from her den.

Chases during the consort period were typically short, and it was always the female who did the chasing irrespective of who made the initial approach. In general, the chases indicated a slightly higher level of aggression on the part of the female than in the give-way interactions, but otherwise were very similar. Instead of walking after a withdrawing male as in a give-way interaction both would break into a run, or instead of sitting watching the male approach the female made a short run in his

direction.

A total of 26 fights were seen during consort behaviour (14 scuffles, 8 wrestles, 3 rump, 1 sparring). The most characteristic of these were the scuffles and the wrestles in which the male made the initial approach. His approach was typically relaxed as in a give-way interaction, but instead of passing, then withdrawing when within 1m of the female he continued without hesitation until right up to her. There then followed a fight of varying intensity ranging from the one fight through brief scuffles to relatively long wrestles. There were obvious sexual overtones to many of these fights, particularly in the wrestles where the male attempted to climb onto the female's back. In the most obvious of these the female rushed at the male (3 obs) but instead of giving way the male met her head on. In one case he managed to get hold of her round the thorax with his forearms, her head under his chest and clung to her as she bit him. He bit at her back, then managed to scramble round onto her back facing the same way as her, clinging to her all the time. The female continued to fight, twisting the front of her body so that she was virtually lying on her shoulders which enable her to bite and claw at the male on top of her, who in his turn was biting at her back. Throughout the fight there were screeches and grunts kept up more or less continuously. Eventually the male broke loose. In another case the male immediately followed and mounted a female when she turned and walked away after a scuffle. In the 2 scuffles on the ground the male approached the female from behind and leapt onto her back, but leapt off almost immediately. There was a tendency for the fights to occur soon after a male climbed into a tree to join a female. Often he climbed the tree and immediately approached her to initiate a fight, after which he tended to settle down into the usual following routine. It was as though he was testing the female's readiness to allow him to mount.

The three rump fights had no sexual overtones. In two the female came rapidly out of her den and caught the waiting male by the rump as he turned to give way, and in the third the female caught the male after a short chase.

When following the female on the ground the male tended to keep 5 to 10m behind her, sometimes dropping back to 20 or 30m and sometimes approaching closer. If he came closer than about 1.5m the female usually reacted by suddenly turning and threatening him, which made him either stop or actually retreat.

Perhaps the most characteristic feature was that he always kept behind the female, rarely did he come level with her. Adult males, on the other hand, though not often seen travelling together, tended to travel level with,and parallel to each other. The male-female situation may be the result of two factors. Firstly, the female virtually ignored the male so the maintenance of the pair was his responsibility. It was easier for him, therefore, to maintain the pair from a position behind the female where he could watch her movements more readily. Secondly, by staying behind the female the male could probably approach closer to her before she responded aggressively. Three observations support this suggestion.

1). A male following 3-4m behind a female suddenly made a dash towards her, and came within 0.5m of her from behind. Just before the dash she had stopped and turned slightly so that he was behind and to one side of her, and the male, instead of bounding straight towards her made a distinct swerve in his approach which compensated for her turn and brought him directly behind her. 2). A male and female were on the ground together feeding, both frequently sitting in upright alert postures but not looking in each other's direction. Gradually the male began to edge towards the female, but only when she was not looking in his direction, until finally he leapt onto her back from about 0.5m when she was gazing into the night away from him. She gave a short sharp screech and spun round, and he immediately leapt off. 3). The third observation clearly shows an advantage of the male approaching a female from behind. A male was following a female and her dependent joey who was following about 1m behind. There had been several interactions involving all three and another two males, and the juvenile had spent some time on its mother's back. The male approached from behind and came between the female and her juvenile apparently without the female

Table 5.1

Distance (m) between Victor and Female Dim-right-eye a) at which she first shows an interest in Victor, b) at which she first shows aggressive behaviour towards him, and c) to which he could approach without any reaction from the female.

a	b	c
1.5	0.5	1.5
2.4	1.5	1.8
1.5	0.5	0.9
2.1	0.6	2.4
0.6	0.3	2.1
1.5	0.6	0.9
0.9	0.9	0.9
0.5	0.3	0.6
1.2	1.5	2.4
1.2	1.5	2.4
0.6	0.3	1.5
1.8	0.5	0.3
0.9	0.6	1.5
1.5	0.6	1.2
1.8	0.5	1.2
1.8	0.1	1.5
0.9		2.4
1.5		0.9
1.2		
1.2		
0.5		
1.2		
0.6		
0.6		
1.5		
1.2		
1.5		
2.7		
1.2		
0.3		
1.2		
no. of obs	31	16	18
Mean	1.26	0.67	1.46
S.E.	0.10	0.11	0.15

Single classification anova (Sokal and Rholf 1969 Box 9.1)

	F	d.f.	P
a,b,c.	8.8755	2,62	<.001+++
ab	13.1316	1,45	<.001+++
ac	1.3182	1,47	>.05 +
bc	16.1313	1,32	<.001+++

noticing that her juvenile had dropped back. He climbed over her rump onto her back, and was on her back before she reacted by spinning round with a screech to dislodge him. It looked as though she had mistaken the male for her juvenile, something she would not have done if he had approached from the front.

One interaction which took place on the ground between Victor and Moon-ear was unusual in that it was much longer (13 min) than any other single male-female interaction and because a stalemate situation appeared to have been reached. The male approached the female whose joey was curled over her back attempting to get in the pouch. When about 2m apart the female gave a k-screech and the male stayed 1m from her. They stared at each other, motionless, for 6 mins, then the male began to slowly move round to one side to come within 0.5m and stopped when she gave a hiss. Again they stood staring intently at each other, the male coming forward and very tense whilst the female stood with one forepaw raised 2-3cm off the ground. The female appeared to relax slightly, first she turned her head to one side then made to move to one side. Immediately the male rushed straight at her but stopped dead when she gave a screech and a grunt. When the male made a forward intention movement the female gave a k-screech. Slowly she moved away from him and stopped about 2m from him, both visibly relaxing with the interaction obviously coming to an end.

5.2113 Female behaviour

Essentially the female played a passive role throughout the consort period. She neither actively sought the male nor, after the male had joined her, did she actively encourage his approach.

Aggressive behaviour directed at the male, when he came within a certain distance was the most prominent behaviour of the female. It took the form of staring at the male, hisses and screeches, and occasionally a raised paw threat. When approached by a male, or vice versa, the female first showed recognisable signs of being aware of the male at a mean distance of 1.26m (Table 5.1). The sign usually consisted of her stopping what she was doing e.g. feeding, grooming, and looking towards the male; or if she

was walking towards the male, looking up to stare at him as she approached. As they came closer her behaviour became more overtly aggressive, e.g. screech or raised paw, at a mean distance of 0.68m (Table 5.1). The closest that a male could come to a female and withdraw without her showing recognisable signs of being aware of his approach was 1.47m which was not significantly different from the 1.26m above. Thus the individual distance as defined by Hediger (1950) between male and female possums was between 0.68m and 1.47m. Beyond the latter distance the female appeared unconcerned at the presence of the male, except when in the same tree she might briefly look in his direction.

Only once did a female appear to deliberately follow a male other than in an aggressive manner. It occurred when Jack had been with Eve for at least 1.5 hr as her consort male, during which time they had at least four encounters. He then came down the tree to the ground and crossed to another tree which he climbed. Eve sat watching him as he moved about on the ground, bounded across to his tree which she immediately climbed and stopped 1.5m below him.

Most significant was the apparent tendency for the female to become more tolerant of the male during the consort period.

The most objective demonstration of this tolerance was the sharing of dens by the male and female. On only 10 occasions was a male observed to share a den with a female, and 6 of these occurred when the female was in oestrus. This tendency becomes clearer when the use of dens by Alec during the 1968 autumn breeding season is examined (Table 5.2). Before establishing a consort relationship with Alice he was always alone when seen emerging from a den in the evening. However, soon after establishing the consort relationship he began to share Alice's den. All six observations of den sharing with an oestrous female involved Alec and Alice, so also did 2 of the other observations, suggesting an individual difference in the tolerance of females towards males.

Other more subjective observations also indicated a greater tolerance of the male by the female, most noticeable after the male had been with

her for a number of hours at night. For example Donald had joined Eve at 02.00 in the morning and stayed with her until she entered her den at 04.30. They had several agonistic interactions but at 04.18 the following comment appeared in my field note book "It looks as though their encounters are becoming milder and that they are beginning to tolerate each other". Since the level of aggression in an interaction is nearly always a reflection of the female's level of aggression, the tolerance mentioned above was owing to a drop in Eve's aggression.

Table 5.2

Use of dens by Alec during 1968 courtship observation period and whether shared. Observations below dividing line made during consort period with Alice.

Date	Den	Den shared with
29.1.68	T318	no one
6.2.68	"	" "
8.2.68	"	" "
12.2.68	"	" "
7.3.68	"	" "
27.3.68	T314	" "
5.4.68	T75	Alice & joey + 12 mth Juv. Female
18.4.68	"	" " " " " " " "
19.4.68	"	" " " " " " " "

5.2114 Consort Vocalisations

The most characteristic call was the quiet appeasement shook-shook given by the consort male when in the vicinity of an oestrous female and the buccal click. An indication of the frequency of the shook-shook call was obtained during a 72 min recording of the consort pair Male 22 and Elga. Male 22 joined Elga 20 mins after coming out of his den and had given 4 shook-shook calls during that 20 mins (12/hr). For the next 52 mins he stayed within 3m of Elga and gave 38 calls, an increase from 12/hr to 45.5/hr. In another example a captive male gave 14 shook-shook calls in 14 mins, a rate of 60/hr, when following a female. However, in another 15 mins observation of Victor when following Female Dim-right-eye in the field, no shook-shook calls were heard. Thus although the call is made by the consort male, sometimes at a rate of up to 1 per min, he does not nec-

essarily make it all the time.

Buccal clicks were rarely heard in the field, even with the aid of the parabola, because of their quietness. However, a caged male when following a female in the 14 min observation already cited gave clicks at the rate of 10.2/min in bouts separated by shook-shook calls, olfactory marking, and pauses. Nineteen click bouts occurred with a mean of 8.7 clicks per bout (range 1-24, S.E. 1.3). It seems probably therefore, that a consort male in the field will give buccal clicks, unless clicks were stimulated by the stresses of captivity.

5.2115 Olfactory Behaviour

Scent probably plays an important role in the consort relationship. Not only did it help the male find the female, but he could probably determine her sexual phase.

Sniffing was performed more frequently by males, and then usually in the vicinity of an oestrous female. Much of this sniffing by the male was at the base of trees and was apparently used to check whether a female was in the tree. Thus in searching for a female, a male who was familiar with the area probably knew from previous experience where to look for a female, but also located her by scent. In the example discussed earlier of Male 33 searching for Eve, scent was obviously an important means of exploring the environment, judging by the amount of sniffing he did. One very characteristic behaviour of the consort male was the way in which he very carefully sniffed a branch at the spot where the female had been sitting for any length of time. Having checked her scent and sometimes marked the branch he then followed her. Occasionally the male would check a den in a similar way after the female had vacated it. It seems probable that the male could detect the phase of the female's oestrous cycle by such scent checking. On 4 separate occasions a male became excited soon after climbing a tree to join a female. His excitement took the form of running up and down the branches until finally he initiated an interaction with the female, usually a fight. This excitement appeared to be triggered by olfactory cues, because the male kept his nose close to the branches as he

ran along them.

Sniffing the body of an individual was rare and was usually in a nose-to-nose situation. Only once did a male come up behind a female and sniff at her cloacal region, to which she reacted by spinning round to face him. Females did little sniffing and only once did a female lift her nose and appear to be sniffing the air as she approached a male.

Olfactory marking in the form of chinning and chesting increased during the breeding season and was often performed when in the vicinity of an oestrous female. It is considered that its main function was to inform other individuals following the female, i.e. other males, of the presence of the consort male with the female.

5.2116 Nightly Duration of Consort Behaviour

In what was considered to be a typical well established consort pair, the male stayed with the female for most of the night. The clearest documented example of this was the observation of Gus and Gert on the night of 8th February, 1966, given in Figure 5.8a in which he stayed with her until just before 02.30. He left her about 150m from their den tree and spent the next hour feeding in another part of his home range. Three weeks later the above pattern was repeated. Gus joined Gert at 19.11 and stayed with her until 03.15 when she left their main feeding tree 200m from her den tree. This time Gus did not follow her down the tree, but stayed in it for another 35 min before coming down and heading for a different den tree to that used by Gert. In both examples Gus ceased to follow Gert well before she reached her den. Either he recognised that she was heading straight back to her den, or his interest in her had waned. Similarly, on 5th March, 1966, Alec joined Alice in her den tree early in the evening and stayed with her until 02.02, by which time they had moved to their main feeding tree, which was also one of their den trees. Alec then left her and when he returned two hours later she was still in the tree. At 04.25 they had a fight and Alice entered the den. Ten minutes later, Alec left the tree and crossed to Alice's other den tree and entered the den. Other less complete examples suggest that the above pattern was common

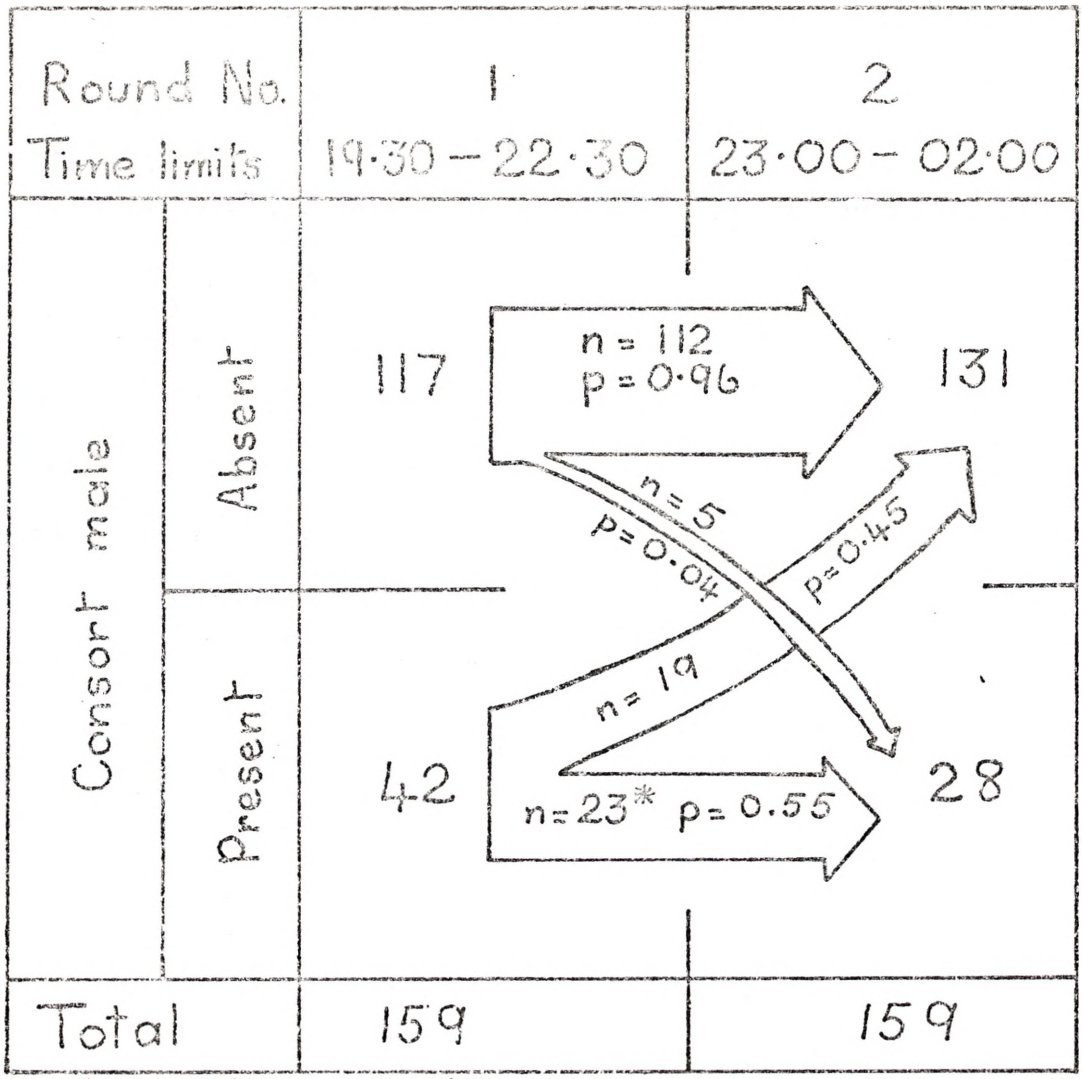


Figure 5.9 : The number of observations of adult females (14 individuals) on two consecutive inspection rounds of the study area during the same night, for a total of 41 nights during the 1968 breeding season, and whether they were accompanied by a consort male. Numbers = observations; thickness of the arrows indicates the probabilities (also shown numerically) of seeing the female with or without a male on the second round.

Mean time between first observation of female on first round, and second observation on second round = 3.29±0.05hrs (range 1.8 to 6.0hrs).

during the consort period.

Nearly all the observations showed the break up of the pair in the early hours of the morning. Sometimes this coincided with the return of the female to her den, but when it did the actual separation took place usually well before the den tree was reached. Leaving the female between two and three in the morning may indicate a general waning of interest on the part of the male, possibly accentuated by hunger, particularly if this had been curtailed earlier in the night by his courtship activities. The only time that a male was observed acting as a consort male right up to the time the female entered her den, was a night when Don didn't join Eve until two in the morning, 2.5 hrs before she entered her den, suggesting that the break down of the pair is a waning of interest on the part of the male at the end of several hours with the female.

A much looser consort relationship, one in which the male did not sustain a close pair with the female throughout the night, was demonstrated by Alec and Alice on 19th September, 1966. Both came out of the same den, but after about 1.25 hrs Alec left Alice and climbed into a neighbouring tree. Although Alec kept within about 50m of Alice he did not actually rejoin her until about 02.0 in the morning for an hour. Then when Alice left the tree to return to her den she took a long unusually circuitous route. Alec made no attempt to follow immediately, but 0.75 hrs later he took exactly the same route, apparently following Alice's scent trail, and finally joined her in the den they had left at dusk.

Once a consort male had joined a female early in the night the probability that he would stay with her for most of the night was obtained from the twice nightly inspection rounds during the 1968 breeding season (see general methods). If a female was seen with a consort male on the first round the probability that she would be seen with a consort male on the second round was 0.55 (Fig. 5. 9), indicating a relatively high divergence from the pattern described above. It is possible that the male may have still been with the female but not seen, however of 11 males seen with a female on the first round and without a female on the second round, eight

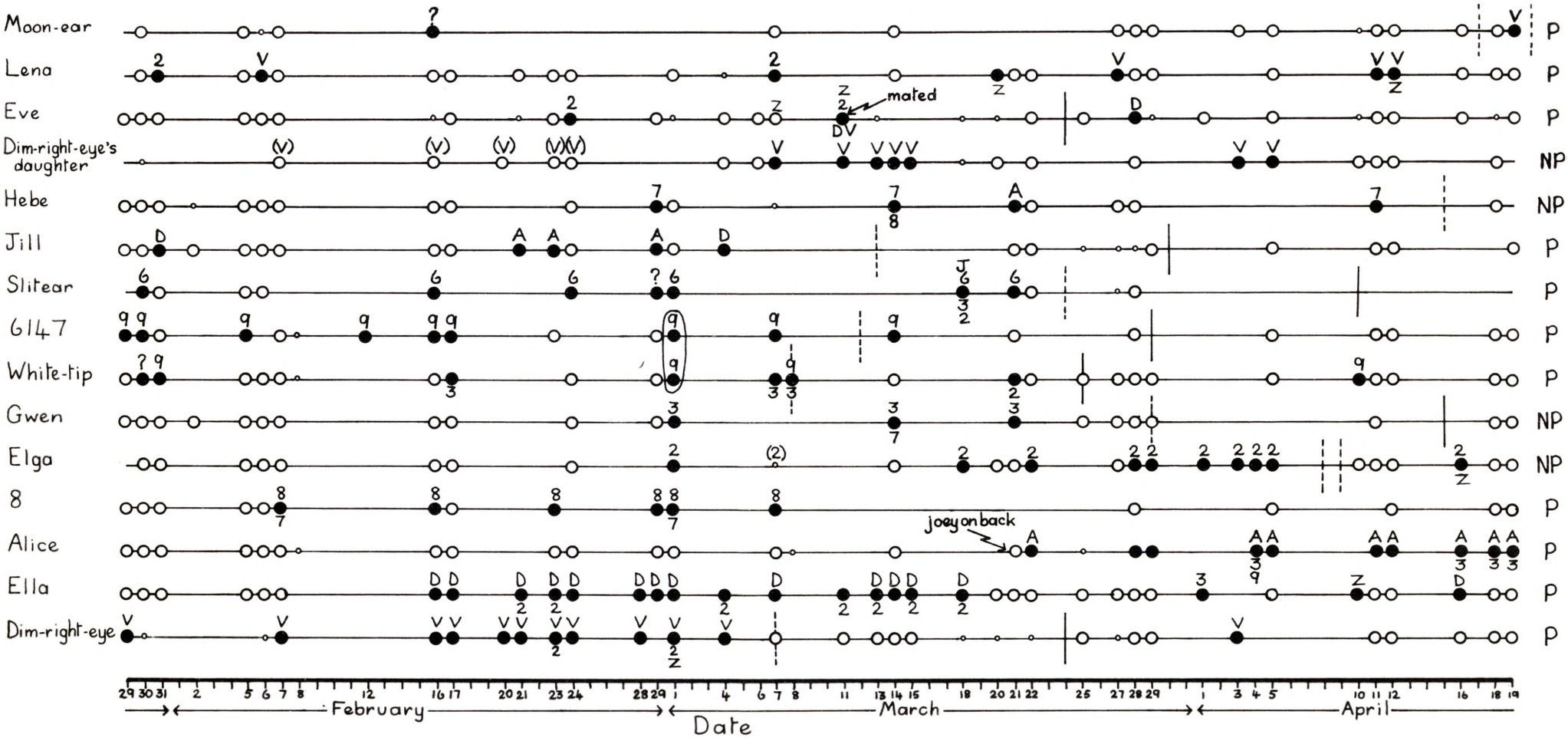


Figure 5.10 : Observations of females during the 1968 breeding season, in relation to the presence of a courting male. Closed circle = female accompanied by male; large open circle = female not accompanied by male; small open circle = female seen alone but not conclusive obs; P = parous female; NP = non-parous female; solid vertical line = estimated date of birth of joey; broken vertical line = estimated date of mating; V = Victor, D = Donald, J = Jack, A = Alec, 2 = Male 22, 3 = Male 32, Z = Male 33, 9 = Male 9, 8 = Male 6228, 7 = Male 7, 6 = Male 6132.

Table 5.3

Individual differences between males in the number of times they were seen with a female on the first round only and with the same female on both rounds.

Male	No. of times seen with a female 1st round only	Both rounds	Total	Partitioned hetereogeneity P.
9	2	3	5	$> .1$
22	7	0	7	$< .005^{+++}$
Donald	6	1	7	$< .05^{+}$
Victor	2	4	6	$> .5$
Alec	0	9	9	$< .005^{+++}$
Total	17	17	34	
Extrinsic expected ratio [1]	0.452	0.548		

[1] obtained from pooled data of all males

G (heterogeneity) = 26.968 pr 4 d.f. $\therefore p < .005^{+++}$

G (pooled) = 0.3116 pr 1 d.f. $\therefore p > .5$

were well away from the female and only three in her vicinity (Mean distance 13m, S.E.8.6) but in a separate tree therefore not classified as a consort male even though possibly still with the female. Nevertheless this still indicated a relatively high divergence from the typical pattern. However, not being with the female did not necessarily mean that the male would not return to the female later that night, as for example in the observation on Alec when he left Alice for 6.5 hrs before rejoining her. If a female was seen with a consort male on both rounds the probability that it was the same male was high, 0.91 (Fig. 5.9) indicating a high degree of fidelity for any one night. On the other hand, if a female was alone on the first inspection round the probability that she would still be alone on the second round was high ($p = 0.96$, Fig. 5.9), indicating that if a male was going to join a female he did so early in the night or not at all.

Time spent by a male with a female each night varied significantly for individual males (Table 5.3). Alec, whether with Alice (7 obs) or Jill (2 obs), was always with the female on both rounds. By contrast, Male 22 was never, and Donald, rarely seen with the same female on the second round. Male 9 and Victor lay somewhere in between. It was Male 22's first breeding season as an established adult male, and Alec was an old well established male which may account for their differences in behaviour with respect to staying with a female. On the other hand, Don who was a well established dominant male, rarely stayed with a female until the second round suggesting that individual differences are important.

5.212 The Consort Period

5.2121 Duration

A male may exhibit consort behaviour towards a female night after night over a period of time referred to as the consort period.

Figure 5.10 sets out the observations of females during the 1968 breeding season. It can be seen that for 3 females in particular (Ella, Dim-right-eye, and Alice) the observations in which they are accompanied by a consort male are clearly demarcated from periods before and/or after when the females were rarely seen with a male. Moreover, males seen with

females outside this period tended to express little if any sexual interest in the female. For example, the 3 observations of Ella with a male in April were all made when the two possums had shared a den tree but not dens, and the male left the tree almost immediately.

Several other females (Female 8, Elga, Gwen, White-tip, 6147, and Slit-ear) show a similar tendency to the above, but one which was not so well defined as in the first three females discussed. Part of this can be attributed to insufficient records, as for example Female 8. Other females, however, with a good series of frequent records indicate that the consort period may be a more intermittent association. Elga for instance does have her consort sightings concentrated, but they are interspersed with sightings when she was seen alone, and Female 6147 and White-tip show a similar tendency.

Not all females were accompanied by a male for any length of time to establish a consort period. The clearest example of this was Eve who was frequently seen and who was one of the two females actually seen to mate. During the 2.5 months observations she was seen with a male or males on only 3 nights, and one of these was when 4 males mated with her on the night of 11th March. The lack of a consort period was substantiated by the history of the males who mated with her. Donald and Male 22 were both acting as consort males to Ella at the time, and only took "time-off" from their relationship with her to mate with Eve. Victor had ceased to be Female Dim-right-eye's consort male a week earlier, and had transferred his consort activities to Dim-right-eye's 11-12 month old daughter. So he also had taken "time-off" to mate with Eve. Finally Male 33 who also mated with Eve had not been seen in her vicinity until four nights earlier, when he was apparently searching for her as described earlier. Other females who may have lacked a consort period entirely were Lena and Moon-ear. The 13 min encounter between Victor and Moon-ear on the ground described earlier took place on 19th April, at about the time when she was estimated to have mated.

The best estimate at the length of a consort period is obtained from

the records of Ella with a minimum time of 31 days (the time between the first and last paired observation of her consort period) and a maximum of 40 days (the time between the records each side of the consort period when she was seen alone). Consort periods of other females were not so well defined but were of similar lengths (Table 5.4).

Table 5.4

Possible maximum and minimum lengths of consort periods based on observations shown in Figure 5.11.

Female	Estimated length of consort period - (days)	
	Minimum	Maximum
3	31	40
Alice	28	-
Dim-right-eye	37	-
23	34	43
8	28	48

5.2122 Relation of consort period to mating

The consort period is a pre-mating relationship with no evidence that it continues for more than one or two nights at the most after mating.

Mating was seen five times during the 1968 breeding season observations, but four occurred on the same night when four males all mated with Eve within 2 hrs of each other, and without any preliminary consort period. In the other observation Male 6228 mated with Female 8 on the 7th March at the end of her observed consort period (Fig. 5.10). As she was not seen again until 21 days later when she was alone, it was not known how long the consort period extended beyond the mating, except that it had finished 21 days later. However, Male 6228 appeared to have lost interest well before this because 7 nights later he was seen acting as Hebe's consort male, and on the 14th and 15th night after mating he was seen alone.

Another 8 matings could be estimated by back dating from measurements of joeys. Six of these occur towards the end of a consort period most

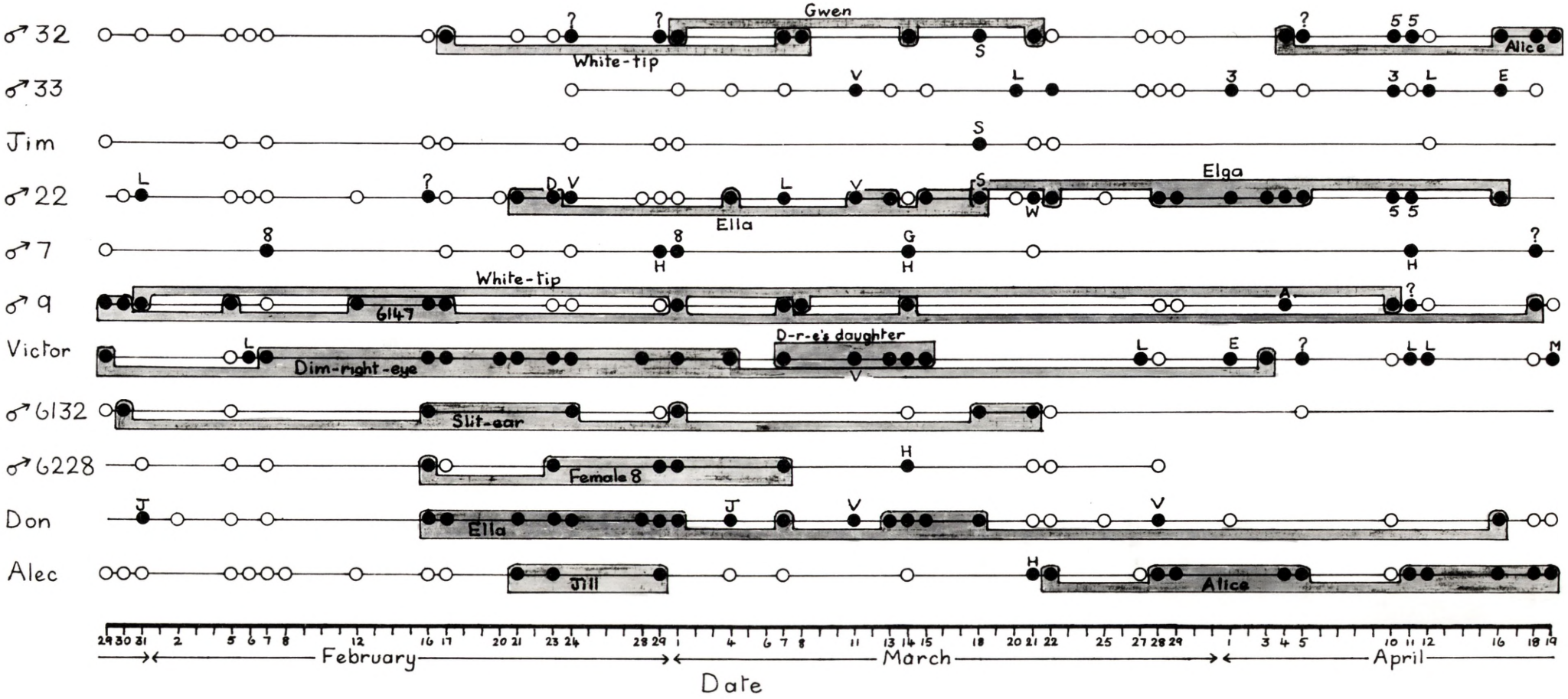


Figure 5.11 : Observations of males during the 1968 breeding season, in relation to the females visited by them. Closed circle = male with female; open circle = not with female; shaded box encloses consecutive observations with the same female; 5 = Female 35, S = Female Slit-ear, V = Eve, L = Lena, 3 = Ella, E = Elga, D = Female Dim-right-eye, W = Female White-tip, 8 = Female 8, H = Hebe, G = Gwen, M = Female Moon-ear, J = Jill.

clearly demonstrated by the records of Elga and Female Dim-right-eye (Fig. 5.10). In the case of Eve she had no consort period, and the observations on Moon-ear suggest an absence of a consort period.

Further evidence that the consort period does not extend beyond mating is provided by the behaviour of Victor. He was Dim-right-eye's regular consort male up to the observed end of the period on the 4th March, and throughout this period he completely ignored Dim-right-eye's year old daughter who shared her mother's den. When he was next seen, on the 7th March, he had completely switched his interest from the mother to the daughter despite the fact that they both came out of the same den. Thereafter for the next four observations he was acting as the daughter's consort male, and he did not return to the mother except for one isolated observation at the beginning of April, in which however he showed no sign of acting as a consort male.

During 1966 Donald was observed to mate with Lesley and to attempt to keep other males from her (see later section on mating sequences). He was also observed next night, and although interested in Lesley, expressed by following and sniffing at the branches she had traversed, this interest was a mere shadow of that shown the previous night both by Donald and several other males.

All the above evidence indicates that the consort period ends soon after mating, probably within 2 or 3 nights, and may even end on the night of mating.

5.2123 Consistency of the pair during the consort period

Throughout the consort period one male acted as the regular consort male to a particular female, although sometimes another male accompanied the female either in place of but more usually as well as the regular male (Fig. 5.10). For example Victor acted as Dim-right-eye's regular consort male, but twice Male 22 and once Male 33 were also present. Similarly Elga was seen only with Male 22 during her consort period, though once with Male 33 after the period. Females 8, Slit-ear, 6147 and Dim-right-eye's daughter all had regular consort males. This together with evidence previously presented (Fig 5.9) that the same male stays with the female

through the night indicates a high degree of consort fidelity.

When accompanied by 2 males, e.g. Ella and Alice, one of the males was seen more frequently than the other e.g. Don and Alec respectively. Also the behaviour of the males clearly indicated that the male most often seen with the female was dominant to the second male who in each case was a young male in his first breeding season.

On examining the records of when and with whom the males were seen paired (Figure 5.11), it is apparent that when acting as a regular consort male to a particular female they do not frequently visit other females;- at least within the time segment of the observations which was from dusk until about 01.00 in 1968. Victor, for example, when acting as consort male to Dim-right-eye was not seen with any other female. Don was twice seen with another female during his consort relationship with Ella; the first time he was in the same tree as Jill but 4-5m below her taking very little notice of her, and the second time was when he mated with Eve along with 3 other males.

When a male ceased to act as a regular consort male to a particular female he occasionally established a consort relationship with a second female. Victor's switch from Dim-right-eye to her daughter illustrates how sudden and complete this switch can be. Male 22 showed a similar switch from Ella, where he was acting as a subordinate consort male, to Elga with whom he was the only regular consort male.

The only male who may have alternated between two females was Male 9, who was seen with Females 6147 and White-tip, but his records are not sufficiently complete to be certain that he had established a consort relationship with both females at the same time.

Donald, on the other hand, appeared to lose all interest in females following his consort relationship with Female 3, despite the presence of two young females in oestrus in his home range. He was seen several times after this consort relationship, but usually alone. On the two nights when seen with a female again he was once with Eve and once with Ella, both of whom had probably already mated. The two young females (Elga and Female

Dim-right-eye's daughter) were sexually attractive because they were accompanied by consort males, Male 22 and Victor respectively. The presence of Victor, a well established adult male, may have deterred Donald's interest in the female. However, in the case of Elga the presence of Male 22 as a consort male did not seem sufficient to account for Donald's apparent complete lack of interest. Male 22 was a young male in the process of establishing a home range, and he had acted in a subordinate role to Donald when both were behaving as consort males to Ella. Thus unless there had been a complete and sudden dominance reversal, unlikely on the evidence presented in the section on male-male relationships, Donald's sexual interest in females appeared to have ceased.

Male 32 failed to establish a consort relationship with any of the females (Jill, Hebe, White-tip and Alice) in his area, and only acted as a regular consort male, in a subordinate role, to Alice at the end of the observation period.

Males 33, 6132, 7 and 6228 were peripheral males, but at least two males, 6228 and 6132, apparently set up typical consort relationships with Females 8 and Slit-ear respectively.

5.2124 Secondary Consort Males

Two females (Alice and Ella) were often seen with two adult males during the consort period; Alec and Male 32 with Alice, and Donald and Male 22 with Ella (Fig. 5.10). Although the males were sometimes seen separately with the female on any one night, they were often seen with the female at the same time. In both cases one male - the primary consort male - was seen more frequently with the female and was obviously dominant to the other male - the secondary consort male. In each case the primary male (Alec and Donald) was an old well established male, whereas the secondary male (Males 32 and 22 respectively) was a young adult either in his first or second autumn breeding season.

Behaviour of the primary consort male was typical consort behaviour, orientated towards the female, with only slight modifications owing to the presence of the secondary male, such as watching him, or the occasional

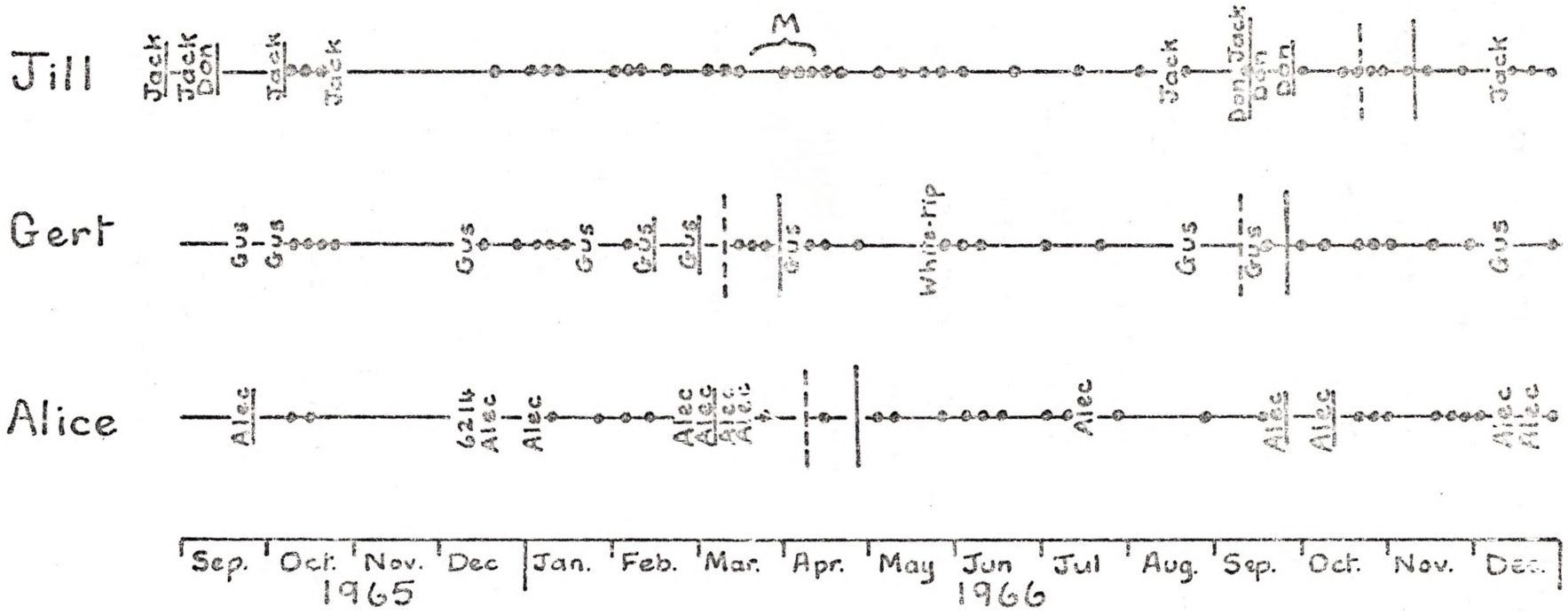


Figure 5.12 : Observations of males in the immediate vicinity of a central female during late 1965 and 1966. Dot = female seen alone; name = individual male in vicinity; name underlined = male sexually interested in female; solid vertical line = birth of joey; broken vertical line = mating.

encounter. The behaviour of the secondary male, on the other hand, was orientated more towards the primary male than towards the female as discussed later in the section on male-male relationships. The primary male was usually closer to the female and from the nature of the branching of the trees this usually meant that he was between the secondary male and the female. If the secondary male was already with the female when the primary male joined the, the former moved away from her, and usually, but not always left the tree. The prior presence of a primary male did not necessarily deter the secondary male joining the consort pair, and once it was the primary male who first left the female.

5.2125 Seasonal occurrence of consort behaviour

Observations on Jill, Gert and Alice during the latter part of 1965 and throughout 1966 indicate that consort behaviour and possibly even extended consort periods are not restricted to the autumn breeding season (Fig. 5.12). For example Alec and Alice were seen as a consort pair during late February early March, then again in late September early October (spring). Similarly Donald appeared to be acting as a consort male to Jill over a period of about 20 days in September.

This consort behaviour in spring occurs at a time when the joeys from the autumn breeding season are beginning to leave the pouch and to ride on their mother's backs, at an age of 4½ to 5 months. However, the number of females who become sexually attractive appears to be relatively low, as only one of the 5 females watched in the spring of 1968 attracted a male. Pilton and Sharman (1962) found that the proportion of female brush-tail possums coming back into oestrus after the removal of young declined after July.

Of the two possible consort periods observed in spring of 1966, Donald and Jack exhibited typical consort behaviour towards Jill. Alec, on the other hand, showed relatively low intensity consort behaviour towards Alice. Although he joined her in her den tree his behaviour lacked the typical following and approaching of a consort male described earlier. The different intensity of consort behaviour of the males may reflect a difference in the

quality of the female's oestrus in that Jill produced a joey, whereas Alice did not (assuming that there was no early pouch mortality). Similarly Eve apparently did not raise a joey after she was seen to mate with Donald.

It appears therefore, that the presence and intensity of male consort behaviour in spring is more variable than in the autumn breeding season. This may be partly a result of a drop in the proportion of females coming into oestrus during spring, and possibly a lower level of sexuality of the males, because Gilmore (1969) has demonstrated that the male prostate gland is smaller in the spring breeding season than in the autumn one.

5.213 Mating Behaviour

5.2131 Mounting and copulation

Mounting was observed 26 times on 8 separate nights. In each case only one female was involved, but the number of males ranged from one to five.

To mount the female the male approached with no preliminary displays and climbed onto her back, either from in front or from behind, and in one case the male leapt onto the female's back from a distance of about 0.75m.

When the male approached the female from the front (10 obs) his approach was usually relaxed and without pausing he climbed over her head, thus forcing it down onto the branch or to one side. He began to turn as he climbed over her so he ended ontop of her and facing the same way. Only once did he climb right onto her so that his nose was over the base of her tail before turning. Twice he grasped the back of the female's neck with his teeth as he mounted but released his grip once facing forward. The female usually acted aggressively (7/10 obs) by screeching and/or giving a raised paw threat of varying intensity. This threatening behaviour had little effect on the male who in only one case retreated, to approach a second time before mounting, nor did it cause him to pause which was the usual preliminary to the male giving way in this type of approach. Her aggression usually diminished noticeably as soon as the male began to climb onto her back and often disappeared altogether. The action of the male climbing over her head seemed to have a pacifying effect, unless it

was that the female's head was pushed down onto the branch into a position where it was impossible for her to be effectively aggressive. However, in one case the female continued to give subdued screeches as the male mated with her, and there was the example, described earlier in which the male had climbed onto the female's back during a fight which continued even when he was on her back.

When a male mounted from behind (29 obs) he walked up to the female and without pausing climbed onto her back until his chin was about level with her shoulder blades. If she moved forward as he was mounting he was sometimes not successful and slid off backwards, usually to follow and attempt to mount again. Only once did a male actually catch hold of a female's rump in an attempt to prevent her from moving away from him. The female showed little or no aggressive behaviour when the male mounted from behind which contrasted, though not significantly, to her behaviour when he mounted from the front (Table 5.5). Only twice did a female show overt aggression, once in the example already cited of the female apparently mistaking the male for her joey, and once when a female gave a short hiss just before the male mounted.

Table 5.5

Relationship between orientation of male mounting female, and female aggression.

Orientation of male mounting	Female Aggression Present	Absent	Total
From in front	7	3	10
From behind	2	7	9
Total	9	10	19

$G = 2.704$ 1 d.f. $p > .05^{+}$

In two observations the male and female first met face to face, before she turned and walked away from him. He followed and mounted her from behind. In one there was a very mild scuffle before the female turned.

In the other the male very gently patted the face of the female with a front paw, and she responded by turning her head to one side then by turning and walking slowly away from him. It is possible that by turning her back to the male the female was inviting the male to mount by avoiding a face to face confrontation.

Twice a male gently placed his paw on the female. In one a consort male who was sitting close behind and slightly below a female slowly reached over and put his paw on her back. She responded by jerking round with a screech and a raised paw and the male sat back. In the other observation a male came up behind a female and stopped immediately behind her. He then reached out and put his paw on the female's joey who was clinging to her back but at that instant another male came up behind the first and chased him away. This paw-on-partner appeared to be an intention mounting movement, not an aggressive one, and may be a means of testing the female's readiness to allow the male to mount.

Once mounted the male clung tightly to the female's back with his fore legs circling her thorax or abdomen and his hind feet grasping her hind legs. The ventral surface of his chin, thorax, and part of his abdomen he kept tightly pressed against the female. Twice a male (two different individuals) appeared to grasp the female's nape with his teeth as he clung to her, and neither of these observations followed the neck bite described as the male climbed over the female's head when mounting.

To achieve intromission the male sometimes moved back so that his fore legs gripped the female's flanks justin front of her hind legs and his body was curved over her rump with his hind feet still gripping her hind legs. When the male was manoeuvering to achieve intromission the female sometimes walked out from under him,indicating that his hind feet loosened their grip as he moved back. The female did not adopt any special position such as lordosis which is adopted by female bandicoots of the genus Perameles (Stodart 1965, Heinsohn 1966) or lateral displacement of the tail to help the male achieve intromission. Instead, the male tended to move slightly to one side of the mid-line on the female's rump in a manner

similar to that of the kangaroo Megaleia rufa (Sharman and Calaby 1964).

Pummelling was an action pattern sometimes performed by the male when clinging to the female's back. It consisted of rapid up and down movements of the front paws with the two limbs working alternately. The paws appeared to grasp and let go of the fur on the female's flanks. Thus it was an action akin to kneading, one that was rapid in comparison to the kneading action of a domestic cat, but not so rapid as to be described as vibration.

Pummelling was seen three times. In one observation the male mounted the female, pummelled her flanks, then overbalanced to one side so that he scrambled off and sat on the branch behind her. This sequence of mounting, pummelling, and overbalancing (the female did not appear to be dislodging him) was repeated several times without the male beginning to pelvic thrust. In a second observation the male pummelled between bouts of copulation while in the third the male mounted, pummelled briefly then began pelvic thrusting.

Pelvic thrusting usually followed a slight pause after the male had mounted, unless it was preceded by pummelling. Sometimes the male dismounted without pelvic thrusting, either because he overbalanced, or was pulled off by another male, or because the female walked out from under him before he could start.

Pelvic thrusts were given in bouts of approximately a dozen thrusts separated by short pauses of up to 0.5 min, and usually with two or three bouts before the male dismounted. Twice the rhythm of the thrusts changed noticeably. In one mating the first few thrusts were erratic and short, then they suddenly became regular and much longer. Similarly in the other observation a series of fast short thrusts were followed by longer more vigorous thrusts. Presumably the change in rhythm coincided with intromission.

Although the 8-10cm long fibro-elastic penis of the possum was frequently seen extended actual intromission was seen only once. It was usually inferred to have taken place either by the change in rhythm of

pelvic thrusting, or by the male ceasing his pelvic thrusts to cling to the female for about 0.5 min before dismounting. One bout of pelvic thrusts in which intromission was inferred to have taken place, was followed by an exaggerated heaving of the male's flanks. His flanks moved out then right in as his abdominal muscles contracted. They were held in this contracted position briefly before another expansion and contraction.

A female's reaction to a mounted male was at first docile. She crouched on the branch with her ears laid back and stared straight ahead and in a few mountings she remained like this until the male had dismounted. In others, however, she began to show signs of restlessness expressed by swaying from side to side, or by beginning to move forward slowly along the branch and in one instance the female made a small forward leap of 3-4cm. Also she sometimes began to show signs of aggression which usually consisted of twisting her head and shoulders so that she could direct bites and blows with a fore paw at the male on her back.

Only once did a female not quieten down after the male had mounted. In this case Lesley resisted Donald as he mounted her from in front, and instead of becoming docile she kept up an almost continuous low screech. Suddenly her screeching increased in intensity and at the same time she began to struggle to dislodge the male. First she appeared to shake herself until she tumbled from the branch with the male still clinging to her back, but they managed to hang from the branch by her hind feet and their tails. Then she rushed down the tree, leapt to the ground from a height of about 3m to land very heavily causing Donald to be dislodged. She slowly got to her feet, apparently dazed, and lunged towards Donald two to three times before trotting to a nearby tree with the male following.

5.2132 Post Copulatory Behaviour

When not dislodged by the female or pulled off by another male, the male dismounted to the rear or to one side and sat on the branch within 3m of the female. She tended to take little notice of him, and made aggressive lunges at him or screeched at him only when she had dislodged the male and even then not always. Even when she did show post copulatory aggression

this rapidly disappeared when the male was more than 1-2m from her. Only once did a male sit within 1m of the female after he had dismounted. It was after a mating in which the female had shown no aggression at all before, during, or after the mounting, and the male sat immediately behind her with no more than 1-2cm separating them.

Apart from some aggressive behaviour immediately following a male's dismounting, the female showed no further interest in the male. Two or three times she walked towards a male after a lapse of several minutes and he gave way, but this appeared to have no direct connection with the mating. Usually she sat gazing into the night.

Similarly a male showed virtually no interest in the female once he had dismounted. After four apparently successful copulations a male gave a long chatter not directed at the female. Release of tension has already been suggested as a causal factor of the post copulatory chatter. All four long chatters followed matings in which the female had behaved aggressively towards the male when he mounted, and in three she also behaved aggressively when he dismounted. A brief chatter was once given by a male following a mounting in which the female displayed only very mild aggression. If, as has been suggested, the long chatter represents the release of tension after the socially stressful situation of mating, then the observation that long chatters followed matings in which the female behaved aggressively i.e. the more stressful matings, agrees with this suggestion. This is further supported by the observation that following the only mating in which aggression was totally lacking the male did not give a long chatter. On the other hand, three matings in which the female did behave aggressively were not followed by a long chatter. If however, we look at the individuals involved it can be seen that all matings in which the female was aggressive, but the male did not chatter, included Donald as the male. (Table 5.6). Either he was incapable of chattering, not likely since he gave a brief chatter after one mating, or he may not have been under so much tension during the mating. Donald was at the top of the dominance hierarchy amongst males, and may also have been under relatively less social stress during

his interactions with females.

Table 5.6

The relationship of the male post-copulatory chatter to the level of female aggression during mating, the presence of other males, and the identity of individuals

Individuals Male	-	Female	Level of female aggression	Other Males Present	Post-copulatory chatter
?	-	?	Medium	Yes	Long
33	-	Eve +	Medium	"	Long
22	-	Eve +	Medium	"	Long
Victor	-	Eve +	Medium	"	Long
Donald	-	Eve	Low	No	Brief
Donald	-	Eve +	Medium	Yes	None
Donald	-	Jess	Medium	No	None
Donald	-	Lesley	High	Yes	None
6228	-	8	None	No	None

+ All within 2 hours of each other.

Grooming was observed after three matings once by a male and twice by females. One of the females thoroughly washed her cloacal region for about 2 min. In the other two instances the grooming was general and not directed at any one specific area.

5.2133 Duration of Mating

Time spent by the male actually mounted was brief and varied from about two to four minutes. One which was carefully timed lasted 3.5 min.

In three observations of mating in which the pair were not disturbed by another male, the male mounted the female twice in the space of 10 to 20 minutes. In one the time between mountings was less than 0.5 min., whereas in the other it was 16 mins.

5.2134 Example of Mating

An example of an apparently successful mating which shows many of the features described, is given in the following protocol. It is one which

occurred in the absence of other males and in which the female showed mild aggression.

26.9.67 19.06 Donald climbs the tree, sniffs and chests it, then goes straight up to where Eve is sitting. As he approached Eve her joey shot up the trunk, but Eve remained seated 10-15 ft. up the tree. There has been no vocalization and Eve has shown no aggressive behaviour. Donald stops 3-4 ft from her. Eve climbs higher in the tree and Donald follows, climbs onto her back and immediately begins pelvic thrusting. However, Eve walks out from under him and goes out along a branch. Don follows and she stops then turns to face him, but without even a pause he pushes her head to one side and climbs onto her back, turning as he does so to face forward. Again he immediately begins pelvic thrusting. Eve sits and makes no attempt to escape. No vocalisation. He stopped pelvic thrusting for 5-10 secs then started again. She is sitting.

19.09+ Donald stops pelvic thrusting and dismounts and Eve moves along the branch. He places a fore paw onto her rump, but she jumps onto another branch about 1 ft higher and is sitting looking down at him. Don climbs onto the branch and they meet face to face. There is a short scuffle then Eve turns and walks away along the branch. Don follows and climbs onto her back (19.09¼) as she continues to walk - no vocalisation - and begins pelvic thrusting. 19.09½ still pelvic thrusting. I can not see whether intromission has occurred. Eve making no attempt to get away or dislodge Donald. He is giving much harder and longer pelvic thrusts now - before they had been fast and short - this possibly occurred at intromission. 19.10 he is clinging to her back not pelvic thrusting. 19.10¼ started pelvic thrusting again, long thrusts, Eve in the same position, not moving and no vocalisation. As far as I can tell no pummelling by Don. 19.11 he stops pelvic thrusting, but starts again 10 secs later - long hard thrusts. She moved a little, Don still pelvic thrusting. They have their backs to me so I can see only Don, and Eve's ear. 19.11½ she is moving about more now, he is hanging on but she does not appear to be trying to dislodge him. Now facing me. 19.12 Eve moving more violently from side to side on the branch and twisting round to bite at Don, but she faces forward again almost immediately. Donald is clinging to her back and it looks as though he is grasping the nape of her neck with his teeth. She is moving along the branch. 19.12¼ Eve suddenly gave a little jump forward, but he is still holding on. There is a fight developing. 19.12¾ Don gets off and gives a short chattering grunt. He moves down the branch and is now 4ft from her. She begins to wash her cloacal region. He is sitting looking in my direction and Eve's joey is about 6 ft above them on the main trunk. Eve stops washing and scratches herself with a hind foot. 19.13½ she moves towards Don and then sits 2 ft from him looking at him, while he is hunched on the branch looking towards her. Eve grooming again, Don sitting. Don moves towards Eve whose tail is twitching slightly as she looks towards him. Eve washing cloacal region, tail twitching. Don sitting looking at her. 19.14 Don starts to groom.

+ Timing obtained from play back of tape which was left running

throughout the above observation.

5.2135 Mating Sequences and their social context

The behaviour immediately preceding mating is referred to as a mating sequence. It may be little more than a single mounting by a single male, as given in the preceding example. Or it may involve multiple mountings and several males. For convenience the sequences are divided into single male and multiple male sequences, and in the latter the interaction of males amongst themselves may be considerable.

The social context of the sequences is examined because differences between the sequences can be explained by differences in the social context.

A total of eight mating sequences was observed, but only the first two described below apparently in their entirety.

5.21351 Single male sequences

The mating between Donald and Eve already given as the example was one of the single male sequences, and probably typical of many. A similar sequence occurred when Donald mated with Jess, except that she appeared less willing to mate. When he climbed into the tree to join her she moved away from him. After a chase he caught and mounted her, but she managed to break free. He again chased and caught her by the rump, this time apparently mounting successfully. Throughout the interaction she appeared to be nervous of him, possibly because she was a young female (23 months). She also showed some aggression but quickly quietened once he was properly mounted.

Neither of the above sequences appeared to be preceded by a consort period. Eve had been seen on four separate nights in the month before she mated, and although males (not Donald) had twice been in her general vicinity they had not been with her. Jack had been seen following Jess and giving courtship vocalisations a month before she mated, but on three subsequent observations she had been alone, and Jack appeared more interested in Ella. Donald had not been seen in her vicinity and his visit to her represented a northern extension of the area he was usually seen in.

A third sequence differed from the two above in that agonistic behaviour, especially female aggression, appeared to be completely lacking. It is

considered to be a significant observation because of this and is therefore described in some detail.

Male 6228 and Female 8 were seen about 3m apart in a tree and when she moved through the canopy to the next tree he followed. He trotted along the branch towards her and climbed onto her back, without the slightest aggression on her part being detected. They disappeared behind the tree trunk and by the time I had moved he was off her back but sitting very close to her, no more than 1-2cm, and both were looking at me. For the next 15-16 minutes they kept very close and whenever she moved he followed her. There was not the slightest sign of agonistic behaviour and even when she moved towards him when climbing to another branch he made no attempt to give way nor did he show any sign of anxiety. After 16 minutes they met nose to nose and he gently patted her on the face with a fore paw which apparently made her turn round on the branch to face away from him. He climbed onto her back and started pelvic thrusting. About one minute later he dismounted and sat on the branch behind her, again within only 1-2cm and again she showed no antagonism to him being so close. A little later she turned and came back along the branch and pushed past Male 6228 without the occurrence of agonistic behaviour from either of them. He continued to follow and when I left them at 22.32 they were sitting about 1m apart and she was grooming.

This mating sequence was preceded by a definite consort period with Male 6228 as the regular consort male (Fig. 5.10).

The most significant feature was the total lack of agonistic behaviour by either possum, and the tendency for the two possums to act as contact animals, witness the male sitting very close to the female and the female pushing past the male. This tendency to act as contact animals was not observed at any other time throughout the study; the usual behaviour being to act as distance animals with a distinct individual distance of about 1m.

Another feature unique to this mating was the repetition of mounting. Other mating sequences frequently contained more than one mounting, but the repeated mountings were either by separate males or because the first

attempts were unsuccessful. Here both mountings appeared to be successful. Also when I left them after watching for half an hour, Male 6228 had not completely lost interest in the female, whereas in other observations of mating the male did lose interest in the female very soon after mating. It is possible therefore that the two mountings that I observed were part of a series of mountings.

Only a fragment was observed of the fourth mating sequence with one male, and both participants were unknown. However, it appeared to resemble the sequence above in that the female showed no aggression at all when the male mounted, and since it occurred on 16th April, which was towards the end of the main breeding season, it is quite likely that it was preceded by a consort period.

5.21352 Multiple Male sequences

Three of the four sequences involving more than one male (2, 2, and 6 males respectively) were similar in that one male appeared to have established "ownership" of the female and attempted to keep the other males from her. Two of these involved two males and in both cases one of the males was already mounted when first seen. The second male approached the mounted male, the approach being relaxed and direct in one instance, but in the other, the approaching male first stopped 10-15m away in an adjacent tree and gave the occasional low chatter as he gazed at the male who was making rather unsuccessful attempts to mount. In both cases when the second male came to within about 2m, the first male dismounted and rushed at the approacher. In one sequence this led to a wrestle fight and a fall to the ground, followed by a pause of 10 mins during which one male just sat, while the other chattered. The silent male remounted the female, but the other male immediately became agitated, then approached and again another fight followed. The final outcome of the sequence was not observed. In the other sequence the approach led to a roundabout chase in the tree in which the chased male once attempted to mount the female, but was eventually chased to the ground. Once on the ground both males stopped to feed, and this was followed by another chase on the ground and by more feeding near the base of the tree. Finally, after

10-15 mins, the first male climbed back into the tree, successfully mated, then gave a long chatter. The second male no longer interfered but continued to feed on the ground near the tree and apparently ignored the mating possums above him.

The third sequence was like the above two in that one male (Donald) was keeping other males away from the female (Lesley) but differed in that a total of six males was involved and it lasted over a period of about 1.5 hrs. It is described in full below.

I was attracted by a series of screeches and chatters to a tree containing Lesley, her dependent juvenile and two males (Donald and Tony). Male 6181 was in an adjacent tree and Victor was on the ground trotting away from the tree. Soon after I arrived Donald chased Tony, but not right out of the tree, then he crossed to the next tree and chased Male 6181 to the ground. Victor appeared excited as he trotted in a wide circle, up to 100m from the tree, before returning but not climbing into the tree.

The juvenile came down to the ground closely followed by Donald but he soon climbed back into the tree as Lesley had not come down. She came down and caught up with the juvenile on the ground, and Donald followed 1 to 2m behind them, occasionally being threatened by Lesley when he came too close.

Twice Male 6181 approached the three of them on the ground, but each time Donald chased him away. The second time 6181 trotted in a wide circle then chased the juvenile up a tree, while he himself remained on the ground. In the meantime Donald and Lesley had climbed into a small tree about 6m tall. Male 6181 crossed to the small tree, sniffed the base, then rapidly climbed the tree but was met by Donald who came down and chased him back to the ground.

For the next 20 mins the tempo of interactions increased dramatically, with Donald continuously on the run as he chased 6181 and other males away from Lesley.

Having chased 6181 to the ground Donald veered to one side and chased Victor away from the base of the tree. Immediately 6181 bounded back up the tree and without any hesitation mounted Lesley, who offered little resistance

apart from a screech. Immediately Donald shot back up the tree and pulled 6181 off Lesley's back (worry fight) and chased him down the tree, but 6181 immediately climbed back up the tree and was again chased down. Male White-tip, a new unmarked male, approached the tree but was chased away by Donald 2 or 3 times. Donald then trotted across to a tree 18m away up which Victor had chased the juvenile, and began to climb it apparently after Victor. No sooner had Donald left Lesley's tree than White-tip bounded up it and mounted her, but he was immediately pulled off (worry fight) by 6181 who had followed him up the tree. 6181 mounted Lesley without bothering to chase White-tip down the tree, who instead climbed higher in the tree. Male 6181 was almost immediately pulled off Lesley's back (worry fight) by Donald who had rapidly returned to the tree. Donald did not chase 6181, but immediately mounted Lesley himself and began pelvic thrusting - the first male to do so. No sooner had he started pelvic thrusting than he dismounted to chase Victor who had climbed the tree and approached from the rear. They went down the tree to the ground and continued the chase on the ground with Victor loping in a circle of about 15m radius to bring him back to the tree up which he bounded and mounted Lesley. Victor immediately began pelvic thrusting, but was quickly pulled off by Donald (worry fight) who then tried to mount Lesley for the second time. She repelled Donald once before he managed to mount, and although she continued to screech he appeared to achieve intromission. She finally dislodged him by dashing down the tree and leaping to the ground.

Lesley trotted to another tree about 40m away and climbed into it, followed by Donald and White-tip, but not by 6181 and Victor who seemed to lose interest in her. Jack was already near the base of the tree when she climbed into it, and he and the two males that had followed climbed the tree after her. Lesley stopped on a branch about 6m up the tree, Jack went higher in the tree, and the other two males stayed on the trunk below her with Donald above White-tip who was near the base.

For the next 15 to 20 mins Donald spent most of his time keeping the other two males away from Lesley, but making no attempt to mount her again

himself. The tempo of interactions had slowed considerably to a series of rather desultory encounters between the males. Male White-tip kept moving up the trunk of the tree only to be chased down again by Donald, and once when Donald had moved down the tree after White-tip, Jack mounted Lesley. She gave a screech and immediately Donald shot up the tree and pulled Jack off her back (worry fight) and chased him down to the base of the tree. For about the next 10 mins Donald sat about 3m up the tree occasionally giving a chatter as he watched the two males on the ground at the foot of the tree. White-tip and Victor repeatedly started to climb the tree, but when about 1m up Donald moved down the tree towards them and the climbing male retreated back to the ground. The males on the ground took very little notice of each other and even though they spent most of the time within 3m of each other there was only one brief chase. Eventually Jack managed to climb past Donald by keeping to the other side of the trunk, but instead of approaching Lesley he went right to the top of the tree and took no further interest in her.

All mating activities appeared to have ceased 1.5 hrs after the beginning of the observations which had started about half an hour after dusk. So the maximum length of the mating sequence could not have been more than 2 hrs. At the end Male White-tip was still at the base of the tree but no longer attempting to climb it. Donald was sitting low in the tree and looking down at the ground. He was no longer giving brief chatters and was sitting with his head hanging, apparently exhausted after so much activity. Also one eye was no longer reflecting light from the spot light and it was later found to have a deep scratch on the cornea which healed to leave him partly blind in the eye from scar tissue. Lesley was sitting quietly in the angle of a branch and the trunk in such a way that the leaning trunk covered her. She had taken up this position after Jack had been pulled off her back, and it seemed to have been done deliberately, possibly to prevent any further mountings. Jack was just sitting about 3m above Lesley. Donald was successful in preventing the other males from mating with Lesley, because although four of the other males mounted Lesley only Victor began pelvic thrusting and

he was pulled off before he could achieve intromission. Donald was the only male who actually achieved intromission.

Social context of the first 2 multiple male sequences was not known because the possums involved were unmarked. In the third sequence all males had home ranges which normally overlapped or were adjacent to that of Lesley's except Male White-tip who was a new male to the area, but he need not have come any great distance because Lesley's home range was on the edge of the study area. Donald's home range completely overlapped Lesley's and he was the male most frequently seen with her. Nine months earlier Donald had been with Lesley at the top of her den tree when attacked by another male. There then followed a situation very similar to that above with Donald keeping 2 males confined to the base of the tree. Donald therefore had a history of accompanying Lesley, and probably acted as her main consort male even though she was occasionally seen with other males.

As far as I could tell the mating sequence was not preceded by a consort period, because Lesley was seen 9 times on 5 separate nights during the previous month and she was always alone.

I watched Lesley on the following night for 1.5 hrs after she came out of her den to see how the males reacted to her. Donald was the only male to join her and he did so soon after she emerged from her den. He followed, sniffed where she had been sitting, and generally acted like a consort male but he made no attempt to mount her, nor did he appear very determined in his approaches. The next night they were seen separately. Thus, following mating the interest of the males in Lesley waned rapidly, with only Donald showing mild interest for a further night.

The fourth multiple male mating sequence differed radically from the other three. The five males involved made no persistent efforts to keep the others away from the female, and four of them appeared to mate successfully with her. The sequence is given in full below.

Again I was first attracted to the possums by a screech and a grunt, and found Eve in her den tree with Male 33 clinging to her back pelvic thrusting. She struggled and managed to break free, but he mounted again

and appeared to achieve intromission before she crawled out from under him with a screech. He then sat within 1m of her and began a long chatter.

About 30 mins later Male 22 began to climb the tree, at which Male 33 stopped chattering and came down to meet him. They met face to face on the trunk, but Male 22 managed to pass the other male and went straight up to Eve whom he mounted even though she screeched and lashed out at him. He was turning round on her back when Male 33 pulled him off (worry fight), and during the ensuing fight Male 33 fell to the ground. Male 22 again mounted Eve, who reacted as before, and apparently mated successfully because he dismounted voluntarily about 1.5 mins later although there was a screech and a brief chatter as he dismounted. He then moved down the branch 2m and began to chatter loudly. Male 33 was at the base of the tree and also chattering.

Five minutes after Male 22 had dismounted, Donald, who had recently arrived on the scene, chased both Male 22 and Male 33 from the tree. Donald, instead of climbing directly to Eve, searched many of the branches and eventually came face to face with Eve's daughter who was higher in the tree than her mother. He gave way to the juvenile and, about 7 mins after chasing the other males to the ground, approached and mounted Eve. She resisted, causing them to over balance, but she managed to hang upside down to the branch with Donald clinging to her back pelvic thrusting. A few minutes later after some screeches and grunts Donald was sitting 2m in front of Eve, but unlike the other males he did not chatter. Male 33 was still at the base of the tree and giving the occasional chatter, but Male 22 had wandered about 40m away from the tree and was chattering continuously. Another male, 6235, was sitting at the base of a tree 40m from Eve's and was looking towards her tree with apparent interest.

Ten minutes after Donald had dismounted Victor was seen approaching the tree. He sniffed one or two nearby trees before carefully sniffing the base of Eve's tree, which he chested and climbed rapidly. Donald came down to meet him, but after a brief scuffle Victor chased Donald down to the ground. Victor approached Eve at a run and mounted without hesitating

despite screeches from Eve. She walked under a branch which brushed him off, but he immediately remounted and apparently mated successfully. After dismounting, Victor chattered for about 23 mins. Donald, Male 33 and Male 22 had all disappeared; and Male 6235 was still sitting 40m away looking in their direction apparently interested but reluctant to approach.

It was just over two hours from the time that Eve was first seen with Male 33 on her back to when Victor stopped chattering.

The most striking aspect of this sequence was the way in which the four males appeared to take it in turn to mate with Eve, and gave way to the next male with comparatively little resistance. It may have been quite by chance that the matings were spaced, possibly determined by the staggered arrivals of the males at her tree. They all (except for Male 6235) climbed her tree as soon as they arrived, consequently, if they had all arrived at the same time the sequence may have involved more fighting between the males.

As previously discussed, Eve completely lacked a consort male and had no consort period. Male 33 was seen four nights earlier sniffing and marking the trees in the vicinity of her den tree and was apparently either searching for her or checking on her reproductive state. It was, however, the first time that he had been seen in the vicinity of her den although he had been seen feeding in the sheds at the stock yards where Eve also fed. Donald, Victor and Male 22 had all taken "time off" from acting as consort males to other females to mate with Eve whose home range was overlapped by all three of the males' home ranges. Male 6235 lived to the west of the study area on the other side of the 100 to 150m strip of open country which effectively acted as the border of the study area. It was the first time he had been seen in the study area and was seen only once more in the same general region of the study area 10 nights later. His hesitancy in approaching the tree when the other males were there may have been owing to his unfamiliarity with the area and the possums in it. Thus none of the males had regularily accompanied Eve prior to her mating, which was apparently the reason why none of them very seriously tried to keep the other males away from her. As a result four males mated successfully with her.

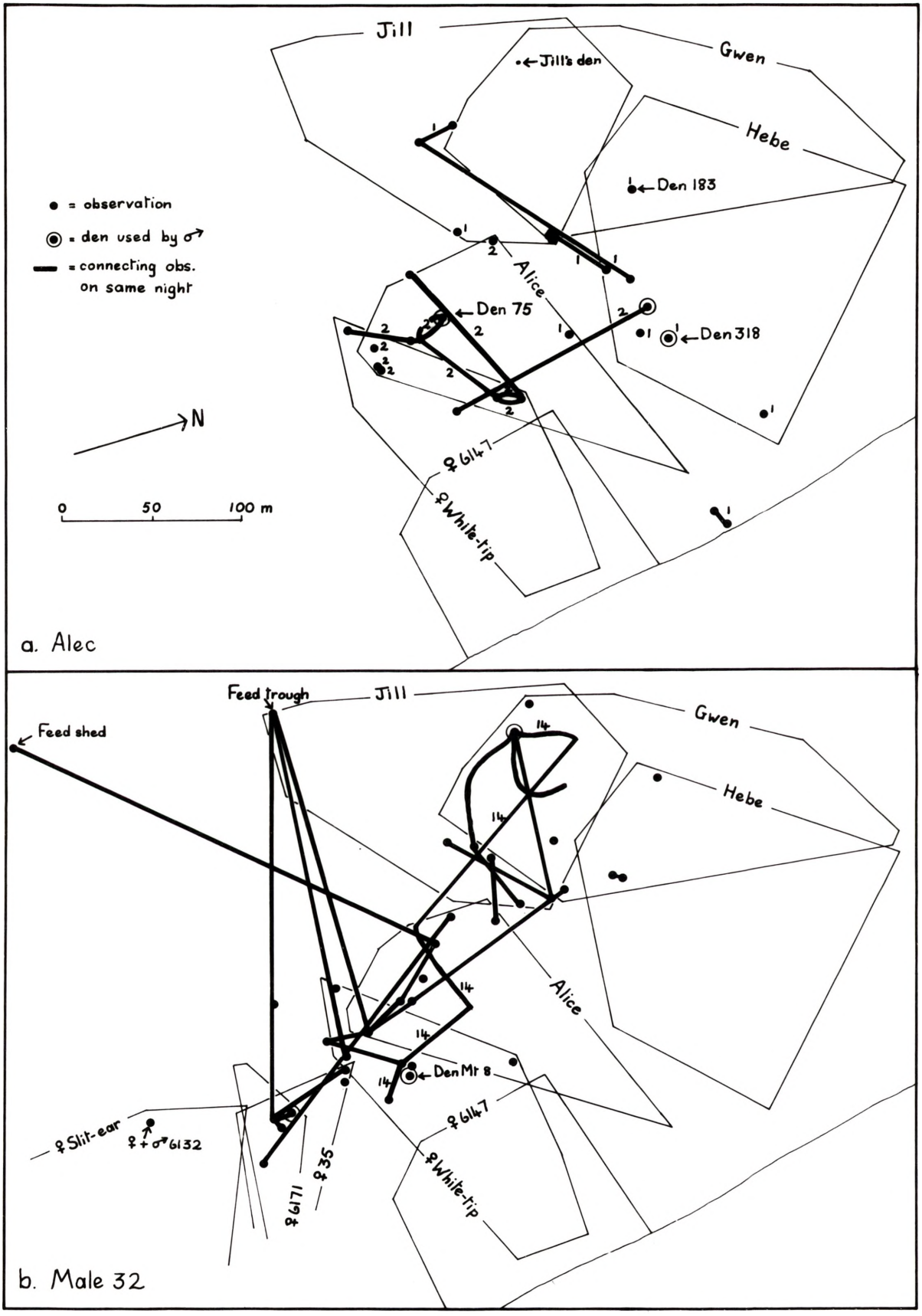


Figure 5.13 : Movements of Alec and Male 32 (heavy lines) during the 1968 breeding season. a) 1 = obs made before 22nd March, 2 = obs made on and after 22nd March, b) 14 = obs made on 14th March. Female home ranges - light lines.

Following mating the males lost interest in Eve. She was seen on another 15 nights during the mating season observations of 1968, but only once with a male (Donald 17 nights later), and he sat 4-5m from her completely ignoring her for the 10 mins that I watched them.

5.214 Activity of males during the 1968 breeding season

Activity of males during the breeding season could be linked to the sexual attractiveness of the females, with variations in this activity apparently related to the age of the male.

Two males (Alec and Male 32) confined their movements to the study area and since they illustrate types of activity at opposite ends of a continuum their activity is described in full.

Alec. He was an old male (9 yrs) with a well established home range that had virtually remained unchanged since the beginning of the study in 1965 and each breeding season he had acted as Alice's consort male.

For the first eight weeks of the 1968 breeding season observations he confined himself to the northern part of his home range, centred on Den 318, with only one marginal and temporally separated overlap with Alice's movements at the time (Fig. 5.13). During this time, he was observed on 12 separate nights and spent long hours just sitting in his den tree, especially during the first two weeks. On 6 of the 12 nights he was seen, he was in his den tree early in the evening. On three of these nights he was also seen from two to three times later in the evening in his den tree, the latest observations being 01.35, 24.46, and 24.30 respectively.

During the third and fourth weeks he was seen with Jill three times and behaving as a consort male, but as these observations were restricted to an eight day period (Fig. 5.11) they did not represent a full length consort period. The fact that he restricted his association with her to a comparatively small overlap zone of their home ranges (Fig. 5.13) without going to her den tree to join her, suggests a rather superficial relationship.

Although two males (Male 32 and Donald) were observed to use Jill's den tree, but not to share a den with her, their presence was not considered to be the reason for Alec's lack of penetration deep into Jill's home range.

Male 32 regularly used the same den tree as Jill, but he was a young adult entering his first breeding season and was clearly subordinate to Alec as shown later. Also Male 32 showed little sexual interest in Jill. Donald's occasional sharing of Jill's den tree represented a considerable northward extension of his home range, and the infrequency of his visits was considered to be insufficient to keep Alec away from Jill. The most likely explanation is an historical one. The den tree used by Jill had previously belonged to Gus and Gert and was a focal point of their home ranges. Jack had moved into the den tree with Gert when Gus had disappeared, but he himself had disappeared about three months prior to the commencement of the breeding season and was replaced by Male 32. Jill had moved in when Gert had disappeared. Both Gus and Jack were adult males of several years, and Gus had been a well established male with only marginal overlap between his and Alec's home range as discussed later in the section on dispersion. It is considered probable therefore that Alec's movements in relation to Jill i.e. his failure to join her at her den tree, may have been a carry over from earlier experiences with Gus and Jack. He was also an old (9 years) male and may have become set in his ways - witness his unchanging home range and his association with Alice over the years.

Alec paid little attention to Hebe who was in her first breeding season, and was seen with her only once. It was the night before he shifted his activities to the southern part of his home range to become Alice's consort male. Hebe's overlap with Alec was not as great as indicated in Figure 13 because she was not observed in the eastern part of her home range until the later part of the breeding season. Her shift from den 183 in the west to den 318 in the east coincided with Alec's shift to the south and his vacating of den 318.

On 22nd March Alec was seen with Alice in the southern part of his home range which represented a complete shift in the focus of his activity. Until observations ceased on 19th April he was seen a further ten times, eight of them with Alice, and always within her home range. The other two observations were when he used den 314, near his previous den 318, and later

the same night when he was seen on the edge of Female White-tip's home range alone.

Alice had come into oestrus late in the breeding season because of a pouch joey she had been carrying over summer, but as soon as her joey began to ride on her back, and presumably when she began to come into oestrus, Alec established a regular consort relationship with her. Before this his interest in the other two females in his area had been superficial, probably not because of any intrinsic differences in the sexual attractiveness of the females, but again probably for historical reasons - namely that over the years Alec had established a very definite relationship with Alice.

Male 32 was a young male, 18 months old, when first caught at the beginning of the 1968 breeding season observations. However, a young male, assumed to be him, had been in the area since the previous October. He was thus in the process of establishing a home range and coming into his first breeding season.

His main axis of activity ran N.W. to S.E. and overlapped the home ranges of five females (Jill, Gwen, Alice, White-tip and Female 35) (Fig. 5.13) He was seen to use three dens along this axis, one at the northern end in Jill's den tree, and two at the southern end. Unlike Alec who only used a part of his home range at any one time, Male 32 used the full length of his home range throughout the breeding season, with a slight tendency to be seen more frequently in the southern part when Female 35 was sexually attractive. Also he would travel the full length of his home range on one night. For example, on the 14th March he was seen coming out of the den at the northern end and travelled to the N.E. to join Gwen in her den tree. Four hours later he was seen travelling from west to east through Alice's home range, and soon afterwards in a tree 20m to the south of den MT8. His four long excursions to the S.W. were made in the last 1.5 weeks of the observation period, and all were to the artificial concentrations of food not to females. He appeared equally interested in a number of females, although it is possible that he established a full length consort relationship

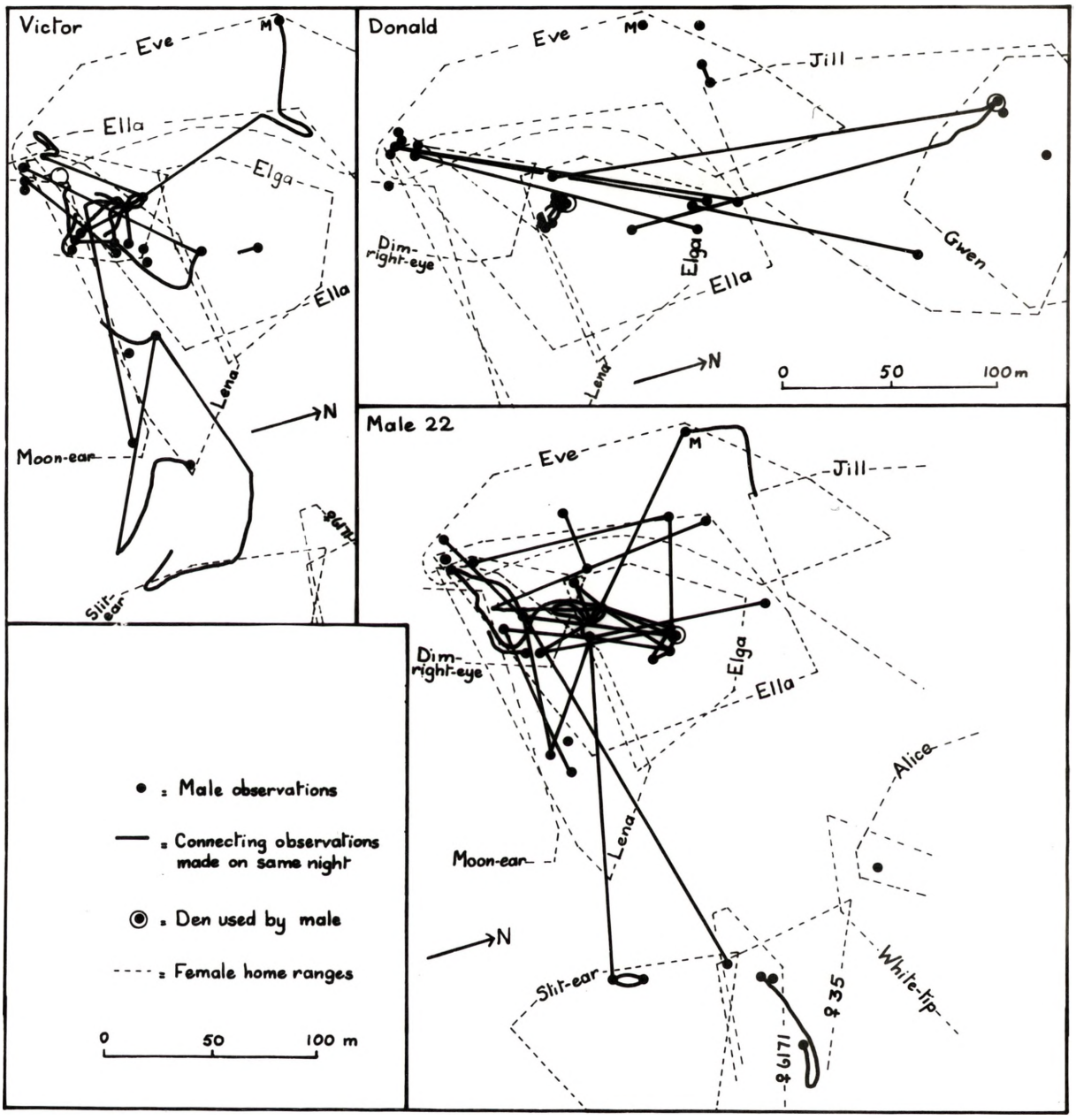


Figure 5.14 : Movements of Victor, Donald, and Male 22 during the 1968 breeding season. Dashed lines = female home ranges, M = mated with Eve on 11th March.

with Gwen (Fig. 5.11). Even if he did, it was interrupted by two consecutive nights when he was seen with Female White-tip, and another night when he was seen with Male 6132 and Female Slit-ear right at the opposite end of his home range, indicating that the relationship with Gwen was not as exclusive as that between Alec and Alice. When Alice came into oestrus he was seen with her several times, as a secondary consort male to Alec, and also with Alice's one year old daughter (Amy). On two consecutive nights towards the end of the study period he showed a great deal of interest in Female 35 at the southern end of his home range, but here also he was subordinate to either Male 9 or Male 22 who showed an equal interest in her.

From the above observations it is apparent that the activities of Alec and Male 32 during the 1968 breeding season differed in a number of ways 1) Alec was more restricted in his nightly movements and made a major shift in his centre of activity, whereas Male 32 continued to range widely throughout his home range; 2) Male 32 visited more females (6) than Alec (3); 3) Alec established an exclusive consort relationship with Alice and showed little interest in the other females, whereas Male 32 was equally interested in several of the females he visited, but perhaps established a loose consort relationship with Gwen; 4) Male 32 was subordinate to all the other males he encountered (Alec and Males 9, 22 and 6132).

Other Males Donald, Victor and Male 22 may not have confined their movements to the study area, but they were sufficiently well known to obtain a general picture of their activity.

Male 22 was a young three year old male whose activity was similar to that of Male 32. He visited many females (9), three of them on one night. His level of activity was high, as indicated by the distance between observations on any one night (Fig. 5.14), and he acted as a secondary consort male. He managed to establish a relatively exclusive consort relationship with Elgs towards the end of the main breeding peak, although on two consecutive nights this was broken when he was seen with Female 35 at the same time

as Male 32. He was subordinate to the older males he came into contact with (Donald, Victor and Male 6228) but was dominant to Male 32 when with Female 35 and may have been of equivalent status as Male 9.

Victor (4.5 yrs old) was similar to Males 32 and 22 in the number of females visited (7) and in having a relatively high level of nightly activity (Fig. 5.14). He differed however, in that he established a relatively exclusive consort relationship with Female Dim-right-eye at the beginning of the breeding season with only one observed diversion to another female right at the beginning (Fig. 5.11). It was not until after this consort relationship with Female Dim-right-eye had finished that he made most of his visits to other females, but without establishing any lasting consort relationship with them.

Donald was an old (7.5 yrs) male, and like Alec was seen with only a low number of females (3). With one of these (Ella) he established an exclusive consort relationship, though he did take time out to mate with Eve, whereas he appeared little interested in the other females (Fig. 5.11). This lack of interest was emphasized by his complete disregard for Elga when she came into oestrus even though his home range completely overlapped hers, and his consort relationship with Ella had ended. It was the subordinate Male 22 who established a consort relationship with her, apparently by default and not because Donald had established a consort relationship with another female, because Donald was seen several times alone and on three of these nights he spent several hours at a time at one or other of the artificial food concentrations. He was however, rather more active than Alec as indicated by his nightly movements (Fig. 5.14), partly owing to his occasional use of Jill's den tree. After the termination of his consort relationship with Ella there was a noticeable decline in his activity.

A trend related to age and consisting of a complex of activity, number of females visited, and the type of consort relationships established is suggested by the above observations (Table 5.7).

Table 5.7

Relationship of age of adult males to sexual behaviour during 1968 Autumn breeding season (Feb-April 1968).

Male	Alec	Donald	Victor	22	32
Estimated Age (yrs)	9	8	5	3	2
No. of females visited	3	3	7	9	7
Consort Relationship	Exclusive	Exclusive	Exclusive	Broken	Broken
Interest in Other females	Low	Low	High	High	High
Night activity	Low	High/Low	High	High	High
Acted as 2nd consort male	No	No	No	Yes	Yes
Dominance status	High	High	High	Medium	Low

It was the three oldest males who established exclusive consort relationships with a female, whereas the two young males appeared more likely to interrupt the consort period to visit other females. Outside the exclusive consort period only the youngest of the three older males (Victor) showed a relatively active interest in other females. Alec was relatively inactive, whereas the three youngest males were more active. Donald changed from a relatively active phase to an inactive one halfway through the observation period. Only the two youngest males acted as secondary consort males. Finally there appeared to be a change in relative status with age, in the sense that while the three older males were not noticeably subordinate to each other, Male 32, the youngest, was subordinate to all other males, and Male 22 occupied a somewhat intermediate position, in that he was dominant to Male 32, but subordinate to the other males.

Thus it appears that as males grow older they rise in status, restrict their interest to fewer females, but at the same time form a more exclusive consort relationship with one particular female.

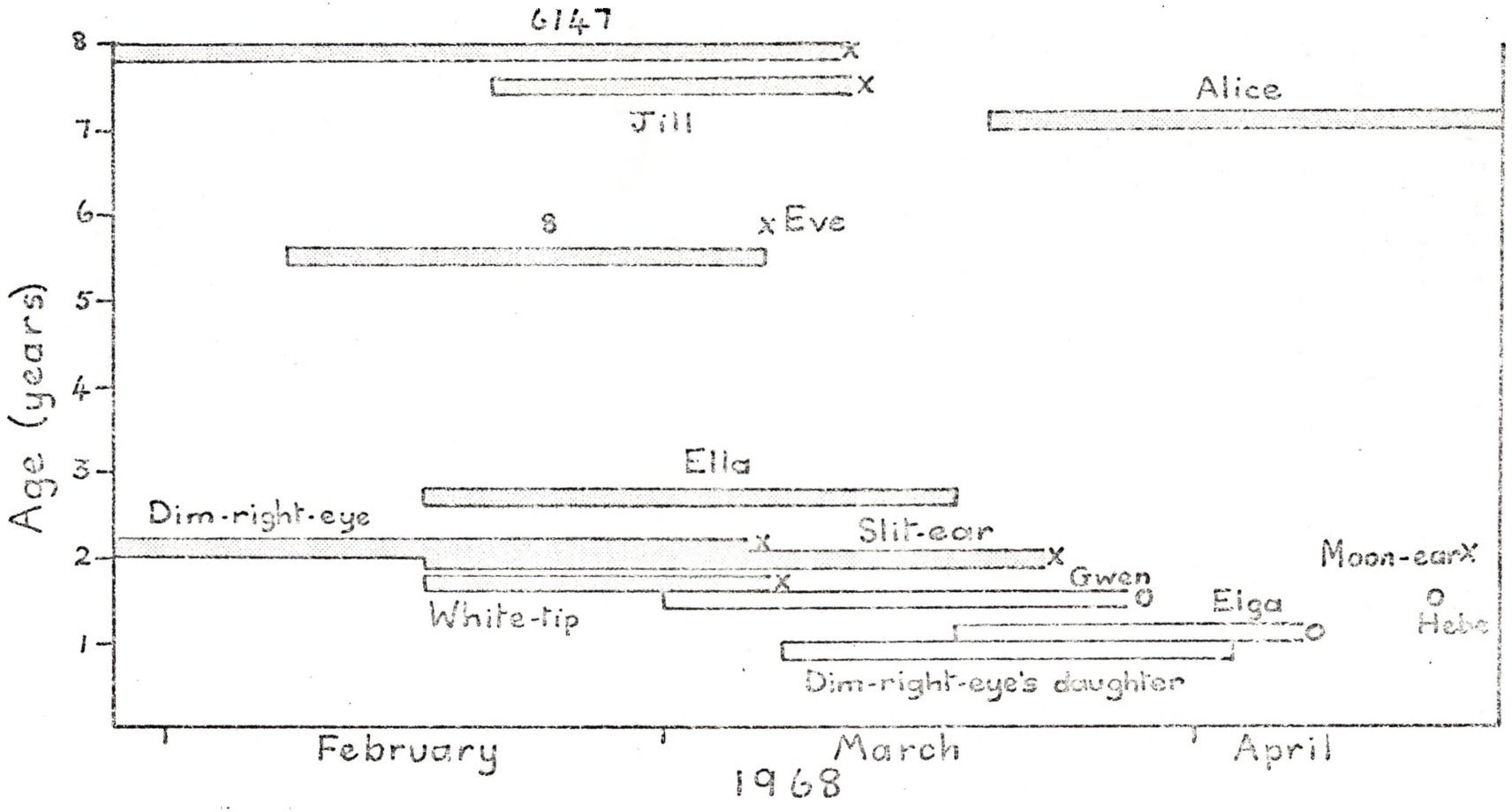


Figure 5.15 : Mating of females in relation to age and consort period. Consort period - parous females shaded, non-parous females unshaded; estimated date of conception, parous female = x, non-parous female = 0.

5.215 Mating in Relation to Age of Females

Young non-parous females tended to mate later in the breeding season than the parous females, and their consort periods to occur later than those of parous females (Fig. 5.15). It is not known whether the explanation for this is purely physical, with non-parous females starting oestrus later than the parous females, or whether it had a social basis. Late starting of oestrus seems the more probable explanation because even young males took no interest in the non-parous females until later in the season.

5.216 Synchronisation of Male Movements to a Female

There were several cases in which more than one male converged on a female, apparently for just one or two nights.

The best documented case already described was that of Eve when five males converged on her, four of them to mate with her. Male 33 had been seen exploring in the vicinity four nights previously, but the other males had not been observed to show any interest. Yet they all converged on her when she was ready to mate, even Male 6235 from across the 100-150m strip of open country.

Similarly Males 22, 32 and Jim were seen at the same time on one night with Female Slit-ear and her consort male 6132. It was a series of screeches and grunts which had attracted me to this group. Although I had not seen Female Slit-ear for the previous 16 nights I had been in the study area several times and not been attracted by any such activity, and I take this to indicate that the male gathering around Female Slit-ear did not last more than two to three nights, five at the most (see Fig. 5.10).

Males 22 and 32 joined Female 35 for two consecutive nights, and Male 9 was also with her on the second night. All three males showed a great deal of interest in her. As above, the congregation of males may have lasted more than two nights but apparently not more than five to six nights.

These congregations are assumed to take place when the female is ready to mate. Certainly this was so with Eve. Female Slit-ear was estimated to have mated six nights after the congregation, and Female 35 on the second night the males were seen with her. Another such gathering occurred on the

night that Donald mated with Lesley and succeeded in fighting off several males.

Somehow, males are able to detect even over considerable distances when a female is ready to mate. For example Male 22 had to travel 165m from his den to join both Female Slit-ear and Female 35. Male 6235 crossed 100-150m of open ground into what must have been a relatively strange area when Eve mated.

There are three possibilities whereby the males know when a female is ready to mate. 1) The female may produce a very powerful scent which acts as a pheromone. However males appear to do very little air sniffing which one might expect if they were attempting to follow an air borne scent. This is not to say that scent may not be a very important cue when deposited on the substrate, as shown by careful sniffing by males of branches where an oestrous female has been sitting. Three to four days preceding ovulation a copious vaginal mucus is produced which may wet the fur around the cloaca during late oestrus or the early postoestrus phase of the cycle (Hughes and Rodger 1971). As ovulation occurs within 48 hours of oestrus these authors consider that the presence of appreciable quantities of free mucus in the cul-de-sac of the median vagina during this period is likely to be functionally important in the maintenance of a sperm reservoir. The production of copious quantities of mucus may well coincide with the period of intense interest in the females by the males, and since it becomes smeared on the fur it may well act as an olfactory cue which is deposited on the branches where the males can detect it. 2) Vocalisations e.g. screeches, grunts and growls, produced when one male interacts with a female may attract other males. The only drawback to this hypothesis is that vocalisations occur during interactions between males and females at other times, yet it is only when the female is ready to mate that other males converge on her. If other males are attracted in this way it implies that they can distinguish the vocalisations produced when a female is ready to mate. One possibility is that when the female is ready to mate the male becomes more determined in his approach and may even attempt to mount, and as a result the screeches

from the female become more vigorous and prolonged. Also this is the time when grunts and growls are likely to occur. I was often attracted to these male congregations by vocalisations. The feature which indicated to me that the situation was worth investigating was the increased frequency of screeches from a particular spot, together with the presence of grunts or growls. It it was possible for me to sometimes recognise when there is a change in male - female interactions there is every reason to believe that the possums can also recognise this. Although several males were usually present whenever I arrived, the vocalisations were probably produced by male-female rather than male-male interactions which tended to be silent. When four males mated with Eve they did not all arrive at once, but came at approximately half hour intervals, so possibly some of them may have been attracted by the post copulatory chatters. The only direct evidence that a male may have located a female by a call was one observation made on Victor. He had been wandering about rather aimlessly, possibly searching for Lena. A screech came from the direction of the female who was accompanied by Male 33. Immediately Victor headed towards the tree they occupied 25m away, climbed it and supplanted Male 33. 3) Males may carry out exploratory excursions to check on the reproductive state of females in their area. For example, Male 33's exploratory excursion into Eve's den area four days before mating with her appeared to be of this nature. Male 22 was seen only once in Female Slit-ear's home range, but this was a month before joining her. Similarly he made an exploratory excursion into Female 35's vicinity, but again this was 2.5 weeks before he showed any overt interest in her. Males do therefore make long exploratory excursions but these were not often seen. During the breeding season, even if a male stayed with a female as her consort male he usually left her one to two hours before returning to his den in the morning, giving him the opportunity to check on other females.

The explanation I favour is a combination of exploratory trips by males to check on olfactory cues left by a female, and vocalisation made when another male is attempting to mount a female, especially when this has not been preceded by a consort period.

5.22 Non-sexual relationships

Certain interactions between males and females were considered to be of a non-sexual nature.

The most obvious of these interactions took place at den trees either in the evening when the possums were emerging, or in the early morning when they were returning to their dens, and most commonly took place between individuals who shared a den tree. An emerging male either gave way to the female in the tree or dashed past her without any intimation of being attracted to the female. Rather, his behaviour was to watch her carefully as he kept his distance by giving way or as he waited his opportunity to dash past her. These interactions mainly took place when the female was not in oestrus.

An aspect of the female's behaviour which was observed several times was for her to examine the male's den soon after he had vacated it in the evening, sometimes approaching his den while he was still in it causing him to hurriedly leave. She sniffed round the den entrance and usually entered the den spending up to about 5 mins examining it. The female at Tyne St. frequently examined a box used by a male and sometimes just sat in the box for several minutes before leaving. On one occasion she urinated in the box. The male on the other hand was never observed to inspect a female's den in such a manner, although he may sniff briefly around the entrance. Away from their own dens both males and females have been observed to thoroughly examine another den in their home range and to scent and mark the tree in the vicinity of the den, presumably to establish some degree of ownership over the den. It is apparently more important to the female to know what individuals are using dens in the vicinity of hers, and to possibly establish her presence by actually entering a den used by a male to leave her scent superimposed on his.

Unlike sexually orientated interactions the non-sexual interactions in a den tree tended to be initiated by the female (14/21 obs), although in most she appeared to ignore the male and only in a few to intentionally supplant him. All the interactions in which the male made the initial

approach (7/21 obs) were dash-past interactions in which the males main concern was to get past the female.

The non-sexual interactions which took place at den trees in the early morning were noticeably more intense than the evening ones with a higher proportion of chases and fights. (Evening:morning - giveway 13:6, chase 4:6, fight 5:10). There was a tendency for the male to make a greater proportion of the approaches (male approach:female approach - evening 7:14, morning 10:10), and on two separate mornings a male rushed at a female to start a wrestle fight in the immediate vicinity of the den. Most of the interactions took place at the den itself when a male was prevented from entering by a female already in the den, or when a male was evicted by a female arriving later. On one occasion Jack was prevented from entering two dens in separate trees before finding an empty den in a third tree.

When a female evicted a male from a den in the morning or prevented him from entering a den, she was not concerned with also chasing him from the den tree, as any chases which did occur were never more than 3m. On one occasion however a female did harass a male from den to den in a tree containing four dens as shown in the following protocol.

14.11.66, 04.01 Gert and Gus. Gus climbed up the den tree and passed within 3 to 4 feet of Gert, but there was no encounter as he passed. He went on up to the crotch of the two top dens and a little way up the spout of one, but then turned and came down again. Possibly Gert's joey is in one of the dens. Gus then went up towards the lower top south east den but just before he reached the den he had an encounter with Gert. I think she had followed and had attacked him. There was a scuffle and Gus came down the spout and gave a short chatter. Gert went up to the den but not right into it. 04.06 Gus jumped across to the top of the glider den and into it. There was a tremendous scuffle and a short sharp screech and soon afterwards Gus came out of the bottom entrance and jumped across to the main trunk.
04.12 Gus is sitting half in the lower top south east den looking down towards Gert who had come out of the top entrance of the glider den and jumped across to the main trunk. 04.13 Gus entered the den. 04.18 Gert bounded up to the den and went for Gus. Gus gave a screech, not the usual screech but one which seemed to convey actual pain, it was almost a squeal. Presumably Gert was biting him. He came out of the den and down to the crotch, and Gert went into the lower top south east den. Gus sat for a while but at 04.19 jumped across to the glider den and entered via the top entrance.

It is apparent therefore that there is competition between males and

Table 5.9

Observations of wins in adult male-adult female agonistic interactions, (a) tested for goodness of fit to an expected 1:1 ratio with G (Sokal and Rohlf 1969, Box 16.1), and (b) for independence of sexuality of the interaction with G (Sokal and Rohlf 1969 Box 16.9).

		No. of wins					
		Asexual			Sexual		
		Obs	%	Goodness of fit (G)	Obs	%	Goodness of fit (G)
Give-way	Male	3	8.8		13	12.5	
	Female	31	91.2		91	87.5	
		34		26.84+++	104		65.81+++
Chase	Male	1	5.9		3	13.6	
	Female	16	94.1		19	86.4	
		17		15.96+++	22		12.97+++
Fight	Male	0	0.0		2	7.4	
	Female	16	100.0		25	92.6	
		16		22.18+++	27		23.17+++
Total	Male	4	6.0		8	11.8	
	Female	63	94.0		135	88.2	
		67		62.58+++	153		101.27+++

Sexual and asexual independence

$G = 11.150$, 7 d.f., $p > 0.1$ n.s.

females for the dens, and a male may even initiate a fight. Nevertheless it was always the female who won the interactions and took possession of the den.

Away from den trees there was no obvious competition between males and females and non-sexual interactions were those which occurred when the female was inferred to be in anoestrus or when she had a joey in the pouch. Most were relatively mild give-way interactions or brief chases (give-way 20, chase 6, fight 1 obs), when the two possums came together during activities such as travelling and feeding. In a few the male showed a mild interest in the female, but this disappeared at the slightest sign of antagonism by the female. The one fight occurred when a male had approached a dependent juvenile who screeched. The screech brought the mother over who then chased and briefly clung to the male's rump as he hurriedly descended the tree.

Fights, in fact, showed a relationship between locality and whether they were sexual or non-sexual. When examining the 1966 results (Table 5.8) all the non-sexual fights took place in den trees, whereas the sexual ones were distributed evenly between den trees and other localities. This supports the contention that non-sexual fights are concerned with competition for dens.

Table 5.8

The relationship between locality and sexual and non-sexual fights between males and females. Only 1966 observations used.

		Sexual	Non-sexual	
Locality	Den tree	5	10	15
	Other	5	0	5
		10	10	

$G = 4.758$ 1d.f. $p < .05$ +

5.23 Dominance

Although the female possum is slightly smaller than the male she consistantly won 87 to 100% of all types of agonistic interactions whether sexual or asexual (Table 5.9). The highest percentages of female wins

occurred in the asexual interactions, though not significantly different from the sexual interactions (Table 5.9). This indicates that the male's subordinate role was not limited just to courtship interactions in which the male continually approached the female then withdrew following an agonistic interaction. It included all situations including competition for dens. In the asexual interactions three of the four male wins involved young females less than 18 months old. In the sexual interactions the trend for a greater percentage of male wins is probably a result of the females readiness to let the male approach and/or the male's greater determination to approach a female when she is ready to mate. For example, after one of the two fights won by a male, the female turned and moved away from the male and allowed him to mount almost immediately. Similarly one of the three chases won by a male occurred prior to mating.

5.24 Discussion

Following of the female by the male, and sniffing at her pouch or cloaca appears to be a general feature of marsupial courtship (Perameles gunni, Heinsohn 1966; Antechinus flavipes, Marlow 1961 ; Sminthopsis crassicaudata, Ewer 1968b; Bettongia lesueuri, Stodart 1966; Megaleia rufa, Sharman and Calaby 1964; Macropus parryi, Kaufmann 1974; and Didelphis marsupialis, McManus 1970) and one which is apparently used to check the female's sexual condition. Trichosurus vulpecula does not follow this general pattern of pouch and cloacal sniffing. Instead the male has transferred this sniffing to the branches where a female has been sitting. It is a modification made possible by the arboreal habits of the possum, since the female when sitting on a branch has the cloaca pressed against the branch, thus transferring scent to it. Its significance in terms of social behaviour is that the male can check the female's sexual condition without coming within her individual distance and thus evoking an aggressive response.

The long-nosed Bandicoot (Perameles nasuta), a strictly terrestrial animal, also deviates from the general pattern, because the male neither sniffs the cloaca or pouch opening of the female nor apparently does it

sniff at the ground where the female has been (Stodart 1965). This indicates that differences occur even in the same genus (Perameles), unless it is a reflection of the different conditions observations were made under.

Soft calls are given by a number of marsupial males when courting a female; clucking by the macropods Macropus canguru, Protemnodon bicolor, P.rufogrisea, Megaleia rufa (Sharman, Calaby & Poole 1966), and Macropus parryi (Kaufmann 1974), a thk-thk-thk by Bettongia lesueuri (Stodart 1966), Da-da-da-da by Sminthopsis crassicaudata (Ewer 1968b), and clicks by Didelphis marsupialis (McManus 1970). All of these calls appear to be equivalent to the male clicks of T.vulpecula and the same or very similar call can be given in other contexts by both sexes, as discussed in the section on vocalisation. No other marsupial, however, appears to have the equivalent of the appeasement shook-shook of T.vulpecula which is exclusively a male courtship call. M.rufa, B.lesueuri, and M.parryi are more gregarious than T.vulpecula and thus may not need a specialised courtship call to enable them to approach a female. Alternatively a male may use an appeasement gesture other than a vocalisation when approaching a female. For example, Ewer (1968b) describes head turning by the male S.crassicaudata to expose his throat and considers this to be an appeasement gesture directed at the female; similarly the male D.marsupialis turns his head, but to present the crown of his head, not his throat, to the female, and McManus (1970) considers that this is an appeasement gesture.

In all the marsupials mentioned above the female plays a very passive role during courtship. She appears to do little more than allow the male to mount when she is ready. For instance, the female M.rufa will stand with her front paws on the ground when she is ready to mate (Sharman & Calaby 1964) and bandicoots of the genus Perameles may adopt a position of lordosis (Stodart 1965, Heinsohn 1966). However, the female ring-tailed possum, Pseudocheirus peregrinus may show overt amicable behaviour towards the male as indicated in the following observation by Marsh (1967). "Complete courtship sequences have not been observed yet, but an apparently receptive

female handled a male's head with her forepaws and appeared to lick the insides of his ears. She was obviously ambivalent in her attitude towards him, however and on several occasions when he approached her she struck at him with her forepaws." The ring-tailed possum is apparently more social than the brush-tail possum in that the probability of finding males and females together in a nest is about 31% (Thompson and Owen 1964) and the male may stay with the female during the raising of her litter, and even carry the young to safety when disturbed (Marsh 1967). Thus the female's handling and licking of the male's head may represent a bonding mechanism.

Consort periods have been observed in both Perameles nasuta (Stodart 1965) and Sminthsopsis crassicaudata (Ewer 1968b) where the male follows the female for a few nights before actually mating with her. In P.nasuta strong attraction was limited to one night only. Also the male was much more strongly attracted to a female when she came into oestrus after a period of anoestrus (Stodart 1965). Three marsupials (Macropus cangaru, Megaleia rufa and Protemnodon bicolor, Sharman, Calaby & Poole 1966) have also been recorded as following the female for a few days before oestrus.

In the whip-tail wallaby (Macropus parryi), which is the only marsupial in which the behaviour has been studied in the field, there is a consort period. Fifteen days was the longest consort period observed by Kaufmann (1974) but they could be as short as 1 day. Thus the consort period was less than half the length of the oestrus cycle of 41-44 days, whereas in the brush-tail possum the consort period more closely approximated the length of the oestrus cycle. The longer consort period of the possum may be more necessary for a solitary mammal than the shorter period of the more social whip-tail wallaby courtship (ibid) as they are in the brush-tail possum. However, in the whip-tail the secondary consort males direct their behaviour towards the female and merely take avoiding action when approached by the primary male. In the brush-tail possum, on the other hand, the secondary male directs most of his attention towards the primary male. This is probably because the movements of the males are dictated by the branching system of a tree, and a secondary male may be more easily cornered.

Trichosurus vulpecula was seen to use two strategies of behaviour leading to mating, probably with a range of intermediates. At one end is the situation where there is no preliminary courtship, but when the female is ready to mate one or more males approach her and mount, irrespective of her aggressive behaviour towards them. At the other end mating is preceded by an exclusive consort period of 30-40 days. A function of the consort period appears to be to eliminate the female's aggression so mating can occur without fighting, as for example when Male 6228 and Female 8 acted as contact animals at the end of the consort period. This is apparently achieved by the male following the female and giving the appeasement shook-shook calls. This reduction of aggression following a consort period was seen only once as described above, but was emphasised by the other matings seen. Before the 1968 breeding season observations started, six mating sequences were seen and all except one involved varying degrees of aggression, with the aggressive screeches and grunts being the means by which I found the mating possums. Thus I expected to see many more matings during the more intensive observations of 1968, but in fact saw only ~~two~~ - the sequence with the four males mating with Eve, and that of Male 6228 and Female 8. It is probable therefore that most of the matings were like the aggression free mating of Male 6228 and Female 8.

Two significant advantages of the consort period are apparent. One; by eliminating aggression at mating it reduces the probability of injury such as Donald's scratched cornea. Two; it increases the probability that it is the consort male who will fertilize the female. It may do this in two ways. Firstly, the consort male by continually following the female will leave his scent superimposed on hers, and he will more likely be there when other males visit the female. In this way he will establish his "ownership" of the female, and other males will come to associate the consort male with the female and learn to avoid her. Secondly, by eliminating aggression at mating, the louder vocalisations (screeches, grunts, growls) are also eliminated, which, as has been suggested, attract other males.

In the case of a relatively young and subordinate male who establishes

a consort relationship with a female in an area also occupied by an older more dominant male, it is not known whether the young male succeeds in mating with the female, or whether the older male displaces him on the night the female mates.

The mounted position of the mounted male is very like that described for Didelphis marsupialis by McManus (1970), except that in Didelphis the neck bite is more an integral part of mounting and the male forces the female onto her side. Jerking or quivering of the forelegs by the male whilst mounted has been noted for two dasyurids (Sminthopsis crassicaudata, Ewer 1968b, and Dasycercus cristicauda Sorenson 1970) Ewer (op.cit.) has suggested that the movements may have a calming effect on the female. The occurrence of pummelling of the Brush-tail Possum early during mounting agrees with Ewer's suggestion, although no change in the female's behaviour was noticed. Neither Reynolds (1952) nor McManus (1970) mention foreleg movements of the mounted male Didelphis marsupialis.

Loss of interest by the male in the female virtually as soon as mating has been achieved, even after an exclusive consort period, appears to be a general feature of marsupial sexual behaviour. In the whip-tail wallaby a male may be attracted to the female for one to two days after oestrus, but no post oestrus pair bond is maintained (Kaufmann 1974). The only marsupial so far studied which shows any form of post copulatory pair bonding is the ring-tailed possum, Pseudocheirus peregrinus (Marsh 1967 and Thomson and Owen 1964), but the observations on this possum are tantalizingly sparse.

The sugar glider (Petaurus breviceps) may form nesting groups of up to 12 individuals (Fleay 1947, and Schultz-Westrum 1965), but it is not known whether these are merely aggregations or of a more social nature.

Thus the courtship behaviour of T.vulpecula, like most other marsupials functions purely to allow mating to take place and not to establish a more permanent pair bond. The only possible exception to this so far observed is the ring-tail possum.

Non-sexual social behaviour in the brush-tail possum was limited to

agonistic interactions centred on den trees. There was no sign of amicable behaviour between males and females such as allogrooming, sniffing, or touching. Sniffing was the main non-sexual interaction between whip-tail wallabies, but allogrooming between adults was not observed (Kaufmann 1974). Kaufmann (loc.cit.) attributes the lack of allogrooming between adults to the fact that whip-tails are among the least aggressive of gregarious mammals. The lack of adult allogrooming is not a general marsupial phenomenon because it has been observed between the small macropod (Setonix brachyurus) (Kitchener 1970 quoted in Kaufmann 1974), thus its absence in the possum can be considered to have a social rather than a phylogenetic basis.

5.3 ADULT MALE-MALE RELATIONSHIPS

5.31 Interactions in the Vicinity of a Female

The majority of male-male interactions (73/90 obs) took place in the vicinity, usually in the same tree, as a female, and nearly all the females (69/73 obs) were judged to be in oestrus. About half (30/69 obs) of these interactions took place during multiple male mating sequences already described, 18 of them in the sequence in which Donald attempted to stop several other males from mating with Lesley. In the remaining 39 observations the female was obviously the focus of attention, although mating was not directly involved. Thirteen were between primary and secondary consort males. In the others a second, though not a secondary consort male, and sometimes a third male joined the male already in attendence with the female. Once, this involved a series of interactions in which one male kept chasing two other males down a tree away from a female.

Usually when a second male joined another male and a female the new arrival climbed the tree without pausing, and without any preliminary threatening behaviour made a low-rush at the other male. A wrestle fight took place and the winner chased the losing male down the tree until the chased male jumped to the ground. Sometimes the chase finished with the chased male clinging to the trunk in the head down position 1-3m from the ground, and the other male 2-3m above him. The lower male then usually

climbed down to the ground although sometimes he turned and began to climb up the tree, only to be chased down once more. These encounters were supplanting interactions, with the newly arrived male attempting to drive the original male away from the female. Even when the attendent male was not between the female and the new arrival the second male made no attempt to go direct to the female, except when the female was ready to mate as in the mating sequences described.

During the fight following the low-rush approach of the second male, the female rapidly climbed higher in the tree and sat peering down at the males. The details of her behaviour were missed because my attention was concentrated on the males.

5.32 Interactions in the Absence of a Female

Relatively few (17/90 obs) male-male interactions were observed to take place away from females. Most were casual encounters with little more than a mild give-way interaction taking place. For example Donald and Gus gradually moved towards each other as they fed on the ground. When about 6m apart Donald stopped and looked towards Gus who continued to feed until 5m away. Then both simultaneously made alarm dashes away from each other. At other times a male leapt onto the base of a tree and gazed in the direction of an approaching male, then jumped down to the ground and moved off when the other was 5 to 15m away.

A few chases took place between males away from females. For instance, Victor approached a tree in which a strange male was sitting about 2m from the ground. He sniffed the base of the tree, then chased the strange male out of it and along the ground for about 15m. On another occasion Jack trotted over to a tree containing a strange young male and began to climb the tree. Jack chased the young male to the top of the tree and down to the ground (long chase). The young male moved across to another tree and after a pause Jack trotted after him. The young male leapt onto the base of a tree and looked down at Jack who then went for him. A 15m chase followed which ended when the strange male spun round to face Jack. They stared at each other briefly, about 5m apart, then both ambled away in opposite

Table 5.10

Outcome of agonistic interactions between individual adult males. Individuals arranged in sequence from the oldest (Alec) to the youngest (Jim). Males of same age bracketed. Draws in parenthesis and not included in totals.

	Alec	Don	6181	Jack	6228	6174	Gus	6103	6132	Vic	Tony	6227	6214	9	22	20	33	32	Jim	Total
Alec													1					3		4
Don			6	6			(1)	1		4	1					11	1	1		31
6181										1										1
Jack	1																			1
6228					1															1
6174												1								1
Gus		(1)										2				3				5
6103																				0
6132																2			1	3
Vic																2		1		4
Tony																				0
6227																				1
6214														1						1
9															1			1		2
22																	1		1	2
20																				0
33																1				1
32																				0
Jim																				0
Total	1	1	6	6	0	1	1	1	0	5	1	3	1	1	1	7	3	3	2	58+(1)

Wins

Losses

directions with all signs of agonistic behaviour having vanished.

Only one fight took place between males away from a female. It was a long drawn out fight lasting for 15 min which started on a fence and finished on the ground. The males were apparently evenly matched and it may represent a rare but vigorous encounter used to determine dominance, or to maintain it. The protocol is given in full.

14.8.67: 20.33 I heard several gutteral chatters and found Donald and Male 6181 on the bull paddock fence at T252. The fence is about 6ft high and of wire mesh. Donald was balanced on top of the fence and chattering and 6181 was clinging to the fence below him. 6181 kept on climbing up towards Don who at times hung head down from the top to reach down at 6181. When close to Don, 6181 usually turned his dead to one side then jumped back down to the ground. Sometimes Don actually lunged at him. Throughout there was a continuous subdued screech, not sure whether made by both. Three times they had a sustained fight, or attempted fight as they were on opposite sides of the wire mesh, and it was always 6181 who broke away. Don made no attempt to follow 6181 to the ground. Once or twice 6181 climbed to the top of the fence and the two males faced each other. In one of these confrontations 6181 lunged at Don, and in the other he shomehow managed to leap over Don's head to land on Don's back, but immediately jumped off and climbed rapidly down the fence. After about 20 approaches by 6181 Don jumped down onto the other male when he was on the ground. Immediately there was dead silence, and although I could not see them in the long grass, they appeared to be perfectly still. After about ½ min 6181 dashed away with Don in pursuit. 6181 stopped briefly by T253 then circled right round the tree with Don after him, both travelling at a steady lope. They again stopped about 10m to south T253 where I could not see them in the long grass, but again there was no movement of the grass. After about 1 min 6181 climbed over the fence into the bull paddock and headed west. No sign of Donald and I thought he must have moved away without me seeing him, so I approached the spot where they had last stopped. As I did so Don dashed away from the spot and galloped alongside the fence, not stopping until level with T903, 75m away. There was no vocalisation from the males while on the ground, but a great deal while on the fence. The pauses on the ground were rather puzzling though they may have been standing facing each other. During the fight on the fence 6181 definitely initiated each aggressive interaction and Don seemed intent on maintaining his position on top of the fence - rather like a game of 'King of the castle'.

5.33 Dominance Relationships

Table 5.10 sets out the recorded wins and losses of male-male interaction, arranged according to relative ages of the males to each other. It is apparent that the older male tends to win the interaction, 53 wins: 4 losses; 1 draw. There may be some bias owing to the second

oldest male (Donald) taking part in over half of the interactions with 31 wins; 1 loss; 1 draw. However, even when his interactions are not included the over all pattern of the older male in the interaction winning is maintained with 22 wins; 3 losses.

Table 5.11

The winner of adult male-male interactions in relation to comparative age and weight of the participants, tested for independence with G (Sokal and Rohlf 1969). 19 males involved.

		Age of winner			
		Older	Younger	Same	Total
Weight of winner	Heavier	37	1	6	44
	Lighter	1	4	0	5
	Same	6	1	1	8
	Total	44	6	7	57

$G = 18.082$ 4 d.f. $p < .005$+++

There was also a strong correlation between weight and age, with the older male in an interaction also being the heavier male (Table 5.11). In interactions between males of equal age it is the heavier male who tends to win, and in interactions between males of equal weight it is the older male who tends to win (Table 5.11).

Dominance reversal in relation to site was not observed. What little evidence there is suggests that it does not occur, and that instead there is a hierarchy between neighbouring males. This seemed to be the case between Donald (9 yrs old) and Jack (7 yrs old). Irrespective of where they met on their home ranges, which overlapped considerably, Donald always won the interaction. This was most clearly shown whenever Jill came into oestrus. Her home range and den lay within Jack's core area, and one would therefore expect that Jack, a well established male, would act as consort male. This was not the case, and it was Donald who acted as consort male, as indicated in the following observations. In September 1965 Donald was seen for the first time in Jill's home range and joined her at her den. Apart from being very alert he in no way appeared nervous or ready to rapidly retreat to his

core area, even though he was well within Jack's core area. Jack, on the other hand, showed no overt interest in the other two even though he came within 25m of the den tree from which screeches were coming. Similarly in September 1966 it was Donald, not Jack, who accompanied Jill when she was in oestrus. A slightly better series of observations suggested that at least one fight early in the series may have established Don's dominance over Jack. On 7th September Jack was in a tree with Jill, well within his home range, when they were joined by Donald who immediately rushed at Jack and after a wrestle fight chased him out of the tree. On 17th Don was with Jill in a tree on the N.E. end of Jack's home range i.e. on the opposite side to Don's normal area of activity, and Jack was in a tree 200m to the S.W. On the 19th Donald and Jack were seen together but not with Jill. They were on the ground and after a mild interaction in which Jack gave way to Donald, they walked parallel to each other, 8-9m apart, for 10 to 30m without any sign of agonistic behaviour between them. On 23rd, Donald, Gus, and Jack were all in the vicinity of Jill's den tree, and Jack appeared distinctly nervous of Donald. Finally, on the 24th September Donald again joined Jill and they travelled 55m over the ground to a tree which they climbed. A little later Jack also came over to Jill's den tree. At first he was very active, trotting from tree to tree, apparently searching. Eventually he appeared to pick up the scent trail of the other two and followed it to the tree they were in. On reaching the tree he made no attempt to climb it, as might have been expected, but instead spent a few minutes investigating the base and looking up into the tree. From his behaviour it was evident that he was aware of the other two but reluctant to climb the tree, presumably because he knew that the dominant male, Donald, was present. This series of observations suggest that a fight, and possibly others, early in the consort period established the dominance of Donald to the extent where Jack would not join Jill, even in his core area, if Donald was with her.

Behaviour of Male 22 towards Donald when they were acting as secondary and primary consort males respectively to Ella, indicates that agonistic

behaviour between males may occur to determine dominance. During their consort relationship with Ella, Donald and Male 22 were seen together on three separate nights. On two of these Male 22 acted as a very subordinate male, keeping well away from Donald with only one give-way interaction between them on one night, and two give-way interactions on the other. On the third night (the second chronologically) Male 22 was more active than on the other two and made several determined approaches towards Donald. However, he never actually made the final rush to start a fight, but stopped about 1m from Donald and stared at him before breaking away and being chased by Donald. Of the seven definable interactions three were chases (2 long) and one a scuffly fight which took place at the end of another chase. The same week Male 22 had joined Male 6132 who was acting as consort male to a female, and several times he approached the older male, but again each time he retreated without fighting when 6132 rushed at him. Possibly Male 22 was testing dominance in both cases without going to the extent of actually trying to establish his own dominance over the much older males.

The progressive establishment of dominance during a series of interactions over a period of about half an hour was demonstrated when Male 22 and a strange male met, probably for the first time. At their first meeting the males peered at each other, about 1m apart, then simultaneously they both turned and moved away from each other. This happened a second time except that Male 22 was a little more hurried in his retreat. In the third meeting Male 22 made a dash-past while the strange male sat and watched i.e. Male 22 was becoming more nervous whereas the strange male was becoming more confident. By the end of the half hour there was no doubt as to the strange male's dominance as he was vigorously chasing Male 22 whenever the latter came close.

Dominance between males is a function of age and weight. It was not determined whether this is due to age per se, which implies older males win because of previous experience, or whether it is because older males tend to be larger than younger males. Age may be important in that young

males coming into the area in an attempt to establish themselves are subordinate to the already established older males. Having thus established a dominance relationship dependent on age this may persist with little change and so retain its correlation with age.

None of the male-male interactions exhibited a strong territorial component. Dominance reversal was not observed, and the only evidence to suggest that one male was attempting to chase the other out of his home range was the 200m chase following a fight in the vicinity of a female. Otherwise the interactions appeared to be concerned with the establishment of dominance, as in the long fight between the two males on the fence, with chasing the other male from the immediate vicinity of a female, or of keeping another male, particularly a stranger, away from the immediate vicinity of the initiating male. This suggests that the immediate function of male-male interactions, especially those in the absence of a female is to establish and maintain dominance relationships and to maintain an individual distance. Observations of males coming within 6m of each other with no apparent interaction suggests a minimum male-male individual distance of 6m, but more frequently this distance was of the order of 15m.

Dominance relationships between males indicate that a hierarchy exists and that it is of the absolute rather than the relative type (Leyhausen 1971), and that it is based on age and/or weight. Linear hierarchies have been recorded for the macropod marsupials Setonix brachyurus (Packer 1969), Megaleia rufa (Russell 1970), Macropus giganteus (Grant 1973), and Macropus parryi (Kaufmann 1971). The situation in the brush-tail possum approaches a linear type hierarchy but it is not strictly comparable to such a hierarchy observed in a group of individuals, because individual possums tend to be relatively evenly dispersed with the older established males having exclusive areas with respect to other males of the same status (Ch. 6.41).

5.4 ADULT FEMALE - FEMALE RELATIONSHIPS

Definable interactions between adult females were rare. When they did come within about 6m of each other on the ground they often peered

intently at each other then continued feeding or travelling, but veering away from each other. Whether females could recognise other females or whether females tended to avoid other possums, irrespective of sex, was not determined.

A total of 24 interactions between adult females were observed, 9 give-ways, 9 chases, and 6 fights.

Ten of the interactions were between mother and daughter when the latter was over one year old (therefore classified as an adult) and in the process of establishing her own home range. Three were between Gert and her daughter Gwen (13 months) when they were sharing a den tree but not dens. After emerging from their dens Gwen watched her mother very carefully and if they came within 2m of each other Gwen rapidly gave way. The remaining mother daughter interactions were between Jill and her daughter Jess over a period of 6 months by the end of which Jess was dominant. By the age of 12 months Jess was using a separate den but still in her mother's home range and still obviously subordinate to her mother. When 15 months old, Jess had an encounter in which she chased her mother from a den entrance, but the situation quickly reversed, with the mother being the ultimate winner. Two interactions were observed between them when Jess was 18 months old, both of which were won by the mother. A month later, however, it was the daughter who won a protracted interaction. In it Jess approached a small tree about 5m high containing Jill; she first chested the base of the tree, then climbed it, sniffing at the branches very carefully, but instead of approaching Jill she stopped on a side branch. For about 5 min they seemed to take no notice of each other, the mother feeding at the top of the tree and the daughter sitting about 2m below her. However, when the mother began to come down the tree with her juvenile following, the daughter moved in towards her. They stopped 0.5m apart, both in the head down position, staring at each other. After about 1 min the mother began to move on down the tree, not hurriedly, but as soon as she moved the daughter jumped across onto the branch immediately behind and above and chased her mother down to the ground. There was a pause as

they watched each other before the younger female rushed at the older one and a leaping fight ensued with the older female breaking away, i.e. losing, and being chased for about 2m. The daughter returned to the tree while the mother remained near the base, probably because her dependent juvenile was still in the tree. Four minutes later Jess came back down to the ground and rushed at her mother and another leaping fight took place with the same result as the first. There was no doubt that the daughter had initiated the interactions and that she had won them, indicating that she was now dominant to her mother. Unfortunately no other interactions were observed between these females to indicate whether this dominance reversal was permanent. However at least two other females were permanently displaced from their dens by their daughters indicating a permanent dominance reversal.

Of the interactions between females other than between known mother and daughter, three were give-ways interactions, seven chases, and four fights. Six of the chases occurred in den trees and were apparently concerned with the eviction of a female from the den tree and not merely the maintenance of individual distance, so inferred because all six chases were long ones, not stopping until the chased female was at least on the lower trunk, and in two the chase continued on the ground for 20 and 40m respectively, both being direct vigorous chases. Two of the den tree chases were in the early morning when the females were returning to their dens, but the other four were earlier in the night, three of them soon after the possums had emerged from their dens in the evening. In the last three chases two older females climbed into trees and chased younger females out of the tree. Both younger females were in their second year and therefore in the process of establishing home ranges of their own and were using dens within the home ranges of the older females by whom they were chased.

On two occasions an adult female was exploring the den tree of another adult female when the owner returned. Immediately the exploring female became agitated and quickly vacated the tree, with only a give-way interaction on one night, but with a chase on the other night.

Five of the six fights between females were on the ground, two between Jill and Jess as already mentioned. All were of the rolling and leaping kind and of varying intensity, and in at least two, one of the females approached with the apparent intent of initiating an interaction.. For example is the fight which took place between Jill and Gert. They were sitting in contiguous small trees about 3m apart and about 2m off the ground. When first seen Gert was sitting staring intently at Jill, who part of the time sat watching Gert and part of the time sat turned away from her. After 5 to 10 min of this Jill came slowly and deliberately down her tree towards Gert then suddenly jumped across to Gert's tree. There was a rapid chase, ending on the ground with Jill catching Gert. The fight that followed was a typical rolling and leaping fight with one long pause in the middle, which terminated by Gert breaking away and unhurriedly walking away as Jill stood watching her. In the other fight the two females gradually came closer on the ground, apparently both feeding, until within 2m of each other. Then one of them ran straight at the other and bowled her over and a brief scuffle took place. The second female broke away, but was again bowled over after a 6m chase before finally managing to escape. In the third fight between two young females there was much leaping into the air and rolling on the ground terminated by a pause, then a brief chase.

None of the five ground fights were followed by a long chase and in at least two the losing female walked in a relaxed manner away from the other. These fights are therefore interpreted as being concerned with the maintenance of individual distance and possibly the establishment of dominance between two relatively evenly matched females, neither of whom give way before the fight. If they were territorial fights, and two did take place in narrow overlap zones of respective home ranges, one would expect the loser to be chased out of the winner's home range and this did not appear to be the case.

Little significance is attached to the remaining interactions, three give-ways, one short tree chase, and one brief rump fight in a tree, beyond

the fact that they were relatively mild interactions between meeting females.

The only obvious territorial component in female-female interactions was when one female chased another from a den tree. Otherwise interactions appeared to primarily concerned with the maintenance of an individual distance which is probably of a similar order to that observed between males, 6 to 15.

As with males, female-female dominance was significantly associated with age and weight (Table 5.12). In one case a daughter (Jess) become dominant to her mother (Jill) and a similar situation occurred in at least two other cases. However, these reversals of the general trend were not frequent enough to significantly effect the trend that older, heavier females are the dominant ones.

Table 5.12

The winner of adult female-female interactions in relation to relative age and weight of the participants, tested for independence with G (Sokal and Rohlf 1969) 10 females involved.

		Age of winner			
		Older	Younger	Same	Total
Weight of Winner	Heavier	11	0	3	14
	Lighter	1	3	0	4
	Same	4	0	0	4
	Total	16	3	3	22

$G = 15.054$, 4 d.f., $p < .005$+++

Table 5.13

Total number of observations of adult-adult agonistic interactions used in the comparison of agonistic interactions

Type of interaction	Sex of Participants		
	Male-female	Male-male	Female-female
Give-way	155	29	9
Chase alone			
Short tree	24	12	3
Long tree	10	11	2
Short ground (interrupted)	3	8	1
Long ground	0	5	2
Fight			
Rump	8	3	1
Scuffle	23	5	-
Wrestle	9	7	-
Worry	-	6	-
Leaping	-	2	5
Sparring	1	-	-
Den	2	-	-

Table 5.14

a) Total observations of the type of interaction in relation to sex of the participants tested for independence with the G-test (Sokal and Rohlf 1969).

Sex of participants	No. of observations Type of Interaction			
	Give-way	Chase	Fight	Total
Male-to-female	83	9	27	119
Female-to-male	69	21	12	102
Male-male	29	41	24	94
Female-female	9	9	6	24
	190	80	69	339

$G = 58.948$ 6 d.f. $p < .005$ +++

b) Partitioning: Sex of participants

Interaction proportions				G (level of significance: 2d.f.)		
Give-way	Chase	Fight		M-to-f	F-to-m	F-f
.70	.07	.23	M-to-f	-		
.67	.21	.12	F-to-m	10.840+++	-	
.31	.44	.25	F-f	14.218+++	7.348+	-
.375	.375	.25	M-m	46.562+++	27.130+++	0.430

c) Partitioning : Type of interaction

Sex of participants proportions						
M-to-f	F-to-m	M-m	F-f		Give-way	Fight
.44	.36	.15	.05	Give-way	-	
.39	.17	.35	.09	Fight	16.512+++	-
.11	.26	.51	.11	Chase	51.504+++	16.194+++

5.5 COMPARISONS OF AGONISTIC INTERACTIONS

5.51 Qualitative

Subtle differences in the type of give-way in relation to the sex of the participants have already been described. None, however, were distinct enough to classify separately.

Chases and fights could be more easily subdivided. Although incidents of interactions were few, the frequencies of various types of interaction (Table 5.13) indicate that some fights were sex dependent. Leaping fights took place on the ground between relatively evenly matched possums both of whom were apparently trying to achieve the same end - the domination and displacement of the other possum. Under natural conditions a male-female leaping fight may not occur because the participants are trying to achieve different ends - the male to mount and the female to stop him. Nevertheless under caged conditions a male was observed making bipedal leaps at a female (Fig. 5.4c), which suggests that this type of fight may be largely a function of its taking place on the ground. Worry fights involved one possum pulling another off a third's back, and in this context is possibly an exclusively male-male fight. However, one observation of a doubtful worry fight between a male and a juvenile of unknown sex suggests that the fight may occur in other contexts.

5.52 Quantitative

5.521 Type of Interaction

The types of interaction with respect to the sex of the participants were tested with the "Likelihood Ratio" or G-test (Sokal and Rholf 1969), and found to be highly dependent (Table 5.14a). Male-female interactions have been divided according to who made the approach vis. male-to-female or female-to-male. The differences attributed to sex were examined more closely by calculating the G values and the ratios (expressed as a proportion) in horizontal partitioning (Table 5.14b). The result in Table 5.14b shows that the male-to-female interactions have a highly significant difference in their ratios of give-way, chase and fight, from female-to-male, male-male and female-female interactions. Similarly female-to-male interactions

Table 5.15

a) Observations (1966 only) of the type of interaction in relation to sex of the participants.

Sex of participants	No. of observations Type of interaction			
	Give-way	Chase	Fight	Total
Male-to-female	28	4	11	43
Female-to-male	14	9	9	32
Male-male	9	20	11	40
Female-female	6	7	3	16
	57	40	34	131

$G = 23.300$ 6 d.f. $p < .005$ +++

b) Partitioning : Sex of participants

Interaction proportions				G Level of significance : 2 d.f.)		
Give-way	Chase	Fight		M-to-f	F-to-m	M-m
.65	.09	.26	M-to-f	-		
.44	.28	.28	F-to-m	5.312	-	
.37	.44	.19	M-m	8.308+	1.246	-
.22	.50	.28	F-f	21.776+++	4.684	1.366

Table 5.16

a) Observations of the type of interaction in relation to the sex of the participants and whether it occurred in months during which conceptions were or were not recorded.

A Sex of Participants	B Interaction type	C No. of observations Conceptions Months with	Months without	Total
Male-to-female	Give-way	79	4	83
	Chase	6	3	9
	Fight	25	2	27
		110	9	119
Female-to-male	Give-way	66	3	69
	Chase	19	2	21
	Fight	5	7	12
		90	12	102
Male-male	Give-way	29	0	29
	Chase	39	2	41
	Fight	24	0	24
		92	2	94
Female-female	Give-way	8	1	9
	Chase	8	1	9
	Fight	5	1	6
		21	3	24
Total		313	26	339
Total	Give-way	182	8	190
	Chase	72	8	80
	Fight	59	10	69

Table 5.16 cont.

Hypothesis tested	d.f.	G	p
A x B independence	6	58.948	$<.005^{+++}$
A x C "	3	8.374	$<.05^{+}$
B x C "	2	8.026	$<.025^{+}$
A x B x C interaction	6	21.162	$<.005^{+++}$
A x B x C independence	17	96.510	$<.005^{+++}$

b) Partitioning : Interactions x period

Period ± conceptions Proportions			G (level of significance 1 d.f.)	
with	without		Give-way	Chase
.96	.04	Give-way	-	
.90	.10	Chase	3.108	-
.85	.15	Fight	7.266 ++	0.704

c) Partitioning : Sex x period

Period ± conceptions Proportions			G (level of significance : 1 d.f.)		
with	without		M-m	M-to-f	F-to-m
.98	.02	M-m	-		
.92	.08	M-to-f	3.480	-	
.88	.12	F-to-m	7.620 ++	1.124	-
.87	.13	F-f	3.956 +	0.512	0.012

differ significantly from male-male and female-female interactions, but there is no significant difference between male-male and female-female interactions. It is evident that both categories of heterosexual interactions have a high proportion of give-ways (.70 and .67) compared with interactions between participants of the same sex (.31 and .375). The male-female interactions differ in having a higher ratio of fights than chases (.23:.07). The female-to-male interactions had the lowest proportion of fights (.12).

In vertical partitioning the types of interaction all differ significantly from each other, with a tendency for give-ways to have the highest proportion of heterosexual, particularly male-to-female, interaction, and for chases to have the highest proportion of male-male and female-female interactions compared with others (Table 5.14c).

Because intensive observations on courtship behaviour were made early in 1968, there could be a bias for heterosexual interactions. However, even the general observations of 1966 show a significant dependence between interactions and sex, with the same, but not always significant, trends (Table 5.15).

Male-female, especially male-to-female, give-way interactions are characteristically a courtship behaviour. To test whether there was a definite change in the ratio of give-way interactions during courtship, interactions during months with no recorded conceptions (Nov., Dec., Jan.) were compared with those of the months with conceptions (approximating a period of courtship). A significant dependence between interactions and period of conception occurred (Table 5.16a).

During the months of conception a higher proportion of give-ways than of either chases or fights occurs though the difference was significant only between give-ways and fights (Table 5.16b). Male-male interactions had the highest proportion of interactions during conception months (.98) though not significantly different from male-to-female interactions (.92), whilst female-female interactions had the lowest (.87) (Table 5.16c).

Because of the highly significant statistical "interaction",

Table 5.17

a) Number of observations of fight types in relation to sex of participants.

Type of fight	No. of observations Sex of participants: Male to female	Female to male	Male Male	Female Female	Total
Scuffle	16	6	5	0	27
Wrestle	8	1	7	0	16
Rump	3	4	3	1	11
Worry	0	0	6	0	6
Leaping	0	0	2	5	7
Total	27	11	23	6	67

G = 50.242 12 d.f. p <.005 +++

b) Partitioning : sex of participants

Fight proportions

Rump	Scuffle	Wrestle	Worry	Leaping
.11	.59	.30	.00	.00
.36	.55	.09	.00	.00
.13	.22	.30	.26	.09
.17	.00	.00	.00	.83

G
(level of significance: 3 d.f.)

	M-to-f	F-to-m	M-m
M-to-f	-		
F-to-m	4.106	-	
M-m	16.894 +++	12.058+	-
F-f	16.696 +++	17.070+++	38.198 +++

interpretation of the data in Table 5.16a must be based on the individual 3-way cells. It is apparent that although male-male interactions have the highest ratio of conception months to non-conception months interactions (92:2), both male-to-female and female-to-male interactions have a higher proportion of give-ways (79 give-way: 6 chase: 25 fight and 66:19:5 respectively) than male-male (29:39:24) and female-female (8:8:5) interactions during the months of conception (Table 5.16a). The high give-way ratios during the months of conceptions are attributed to the male approach and withdrawal courtship interactions.

In male-to-female interactions the female is usually content merely to threaten the approaching male, hence the low ratio of chases. On the other hand, a male may be sufficiently aroused to provoke a fight. With female-to-male interactions the reverse is true. An approaching female is behaving more aggressively than one who is sitting, hence the higher proportion of chases. The male tends to participate in a fight only when he makes the initial approach, hence the lower ratio of fights during the period of conception. In the non-conception period the interactions are often associated with competition for dens, and the male is apparently less inclined to give-way, hence an increase in fights.

5.522 Type of Fight

The different types of fights have a highly significant level of dependence with the sex of the participants (Table 5.17a). Male-female fights have the highest proportion of scuffles which are brief and low in overt aggression (Table 5.17b). Although the two categories of heterosexual interactions do not differ significantly in their fight ratios, male-to-female fights have a higher proportion of wrestle fights (.30) than female-to-male fights (.09) (Table 5.17b). Wrestles are a relatively aggressive encounter and reflect the male's willingness to fight when he makes the initial approach. However when the female makes the approach the male is more likely to turn away, giving a higher proportion of rump fights (.36), than when the male makes the approach (.11). Male-male fights include high proportions of wrestles (.30) and worry fights (.26) both of which are

Table 5.18

a) Number of observations of fights immediately followed by a chase.

	No. of observations Fight followed by chase		
	Yes	No	Total
Male-to-female	6	20	26
Female-to-male	5	9	14
Male-male	18	6	24
Female-female	3	3	6
Total	32	38	70

G = 14.878 3 d.f. $p < .005^{+++}$

b) Partitioning

Subsequent chase proportions			G (level of significance 1 d.f.)		
Yes	No		M-to-f	F-to-m	F-f
.23	.77	M-to-f	-		
.36	.64	F-to-m	0.712	-	
.50	.50	F-f	1.613	0.352	-
.75	.25	M-m	14.154 +++	5.742 +	2.774

Table 5.19

a) Observations of chases not accompanying fights in relation to the length of the chase, site of the chase, and sex of the participants.

A	B	C				
		No. of observations				
Chase	Chase	Sex of participants				
Length	Site	Male to female	Female to male	Male male	Female female	Total
Short	Tree	5	15	11	4	35
	Ground	2	1	9	3	15
		7	16	20	7	50
Long	Tree	2	5	23	6	36
	Ground	0	1	6	3	10
		2	6	29	9	46
Total		9	22	49	16	96

Hypothesis tested	d.f.	G	p
A x B Independence	1	0.854	>.1
A x C "	3	9.404	<.025 +
B x C "	3	5.638	>.1
A x B x C Interaction	3	4.242	>.1
A x B x C Independence	10	20.138	<.05 +

b) Partitioning : length x sex of participants

Chase length proportions				G (level of significance 1 d.f.)		
Short		Long		M-to-f	F-to-m	F-f
.78	:	.22	M-to-f	-		
.73	:	.27	F-to-m	0.086	-	
.44	:	.56	F-f	2.830	3.270	-
.41	:	.59	M-m	4.328 +	6.366 +	0.044

Table 5.2C

a) Observations of the type of approach in relation to the type of interaction and sex of participants. Only relaxed and rapid approach tested for independence with G -- test because of low numbers of other types

A	B	C			
		No. of observations			
Type of Approach	Sex of participants	Type of interaction			
		Give-way	Chase	Fight	Total
Relaxed	Male-to-female	75	7	11	93
	Female-to-male	55	6	5	66
	Male-male	26	13	4	43
	Female-female	7	3	1	11
		163	29	21	213
Rapid	Male-to-female	12	2	10	24
	Female-to-male	7	7	3	17
	Male-male	3	8	12	23
	Female-female	2	2	5	9
		24	19.	30	73
Low rush	Male-to-female	0	0	3	3
	Female-to-male	0	0	1	1
	Male-male	0	0	3	3
	Female-female	0	0	0	0
		0	0	7	7
Deliberate	Male-to-female	1	0	0	1
	Female-to-male	2	1	2	5
Cautious	Male-to-female	1	1	0	2

Hypothesis tested	d.f.	G	p
A x B independence	3	9.143	$<.05^{+}$
A x C "	2	48.036	$<.005^{+++}$
B x C "	6	30.625	$<.005^{+++}$
A x B x C interaction	6	0.212	$>.995$
A x B x C independence	17	88.017	$<.005^{+++}$

Table 5.20 cont.

b) Partitioning : Approach x interaction

Approach (proportions)			G (level of significance 1d.f.)	
Relaxed	Rapid		Give-way	Chase
.87	.13	Give-way	-	
.60	.40	Chase	15.894 +++	-
.41	.59	Fight	42.464 +++	3.686

c) Partitioning : Approach x sex of participants

Approach (proportions)			G (level of significance 1d.f.)		
Relaxed	Rapid		M-to-f	F-to-m	M-m
.79	.21	M-to-f	-		
.79	.21	F-to-m	0.000	-	
.65	.35	M-m	4.440 +	3.850 +	-
.55	.45	F-m	5.006 +	4.696 +	0.666

aggressive encounters. This fact and the presence of leaping fights make male-male fights significantly different from the heterosexual fights. Female-female fights are predominantly of the leaping kind, which may be relatively aggressive when rolling is involved, and are after prolonged.

A fight followed by a chase is considered to be more aggressive, and male-male fights are followed by a chase significantly more often than other categories of participants (Table 5.18). There is a tendency, though not significant, for female-female fights to be followed more frequently by chases then male-female fights.

5.523 Type of Chase

Chases which did not accompany fights were found to be significantly dependent on the sex of the participants regarding length but not where they took place (Table 5.19a). Male-to-female and female-to-male chases were mostly short in duration and differed significantly from male-male chases in this respect. Female-female chases were mainly long in duration but not significantly different to male-female chases (Table 5.19b).

5.524 Type of Approach

A highly significant dependence exists between the type of approach and the type of interaction (Table 5.20a). Give-ways were preceded by a high proportion of relaxed approaches (.87), differing significantly from both chases and fights, the latter having the highest proportion of rapid approaches (.59) (Table 5.20b). Fights and chases did not differ significantly. However, if low rushes, all of which were followed by a fight were combined with rapid approaches, then fights were preceded by a significantly higher frequency of either rapid or low-rush approaches ($G = 6.230 +$ 1 d.f.).

Dependence also existed between the type of approach and the sex of the participant. Heterosexual interactions were preceded by the highest proportion of relaxed approaches (.795 in each case), and female-female by the highest proportion of rapid approaches (.45) though not significantly different from male-male interactions (Table 5.20c).

Since the statistical "interaction" is not significant it can be concluded that male-female give-ways have the highest ratio of relaxed

Table 5.21

a) Observations of the type of withdrawal in relation to the type of interaction and sex of participants. Only give-way and fight tested for independence because by definition chase has rapid withdrawal.

A Type of interaction	B Sex of Participants	C No. of observations Type of withdrawal Relaxed	Rapid	Total
Give-way	Male-to-female	45	40	85
	Female-to-male	28	37	65
	Male-male	12	13	25
	Female-female	2	6	8
		87	96	183
Fight	Male-to-female	3	20	23
	Female-to-male	0	11	11
	Male-male	0	17	17
	Female-female	2	4	6
		5	52	57
Total		92	148	240
Give-way + fight	Male-to-female	48	60	108
	Female-to-male	28	48	76
	Male-male	12	30	42
	Female-female	4	10	14
Chase	Male-to-female	0	10	10
	Female-to-male	0	21	21
	Male-male	0	36	36
	Female-female	0	9	9
		0	76	76

Hypothesis tested	d.f.	G	P
A x B independence	3	12.610	<.01 ++
A x C "	1	32.390	<.005+++
B x C "	3	4.100	>.1
A x B x C interaction	3	7.569	<.05 +
A x B x C independence	10	56.668	<.005+++

b)

Proportions	withdrawal Relaxed	Rapid
Give-way	.48	.52
Fight	.09	.91

Table 5.22

Observations of the type of interaction in relation to the sex of the participants and the site of the interaction

A Site of interaction	B Sex of participants	C No. of observations Type of interactions Give-way	Chase	Fight	Total
In tree	Male-to-female	78	8	25	111
	Female-to-male	69	19	13	101
	Male-male	22	22	20	64
	Female-female	6	5	1	12
		175	54	59	288
On ground	Male-to-female	10	2	2	14
	Female-to-male	3	2	0	5
	Male-male	9	14	3	26
	Female-female	3	3	5	11
		25	21	10	56
Total		200	75	69	344

Hypothesis tested	d.f.	G	P
A x B independence	3	37.640	$< .005^{+++}$
A x C "	2	8.992	$< .025^{+}$
B x C "	6	49.096	$< .005^{+++}$
A x B x C interaction	6	3.564	$> .5$
A x B x C independence	17	99.292	$< .005^{+++}$

b) Partitioning : Interaction x site

site (proportions) Tree	ground		G (level of Significance:1d.f.) Give-way	Fight
.87	.13	Give-way	-	
.86	.14	Fight	0.180	-
.72	.28	Chase	8.694^{+++}	3.960^{+}

c) Partitioning : Sex of participants x site

Site (proportions) Tree	ground		G (level of significance: 1d.f.) F-to-m	M-to-f	M-m
.95	.05	F-to-m	-		
.89	.11	M-to-f	3.346	-	
.71	.29	M-m	22.642^{+++}	10.714^{+++}	-
.52	.48	F-f	24.578	14.924^{+++}	2.864

Table 5.23

a) Observations of interactions in relation to the sex of the participants and the site of the interaction, with trees separated into den trees and other trees.

Sex of participants	No. of observations Interaction site			
	Den tree	Other tree	ground	Total
Male-to-female	55	56	14	125
Female-to-male	64	37	5	106
Male-male	22	42	26	90
Female-female	7	5	11	23
Total	148	140	56	344

$G = 51.422$ 6d.f. $p < .005^{+++}$

b) Partitioning

Site (proportions			G (significance level, 2 d.f.)			
Den tree	Other tree	Ground		F-to-m	M-to-f	F-f
.60	.35	.05	F-to-m	-		
.44	.45	.11	M-to-f	7.464 +	-	
.30	.22	.48	F-f	24.694+++	15.260+++	-
.24	.47	.28	M-m	36.008+++	14.552+++	5.248

approaches, and fights between participants of the same sex the highest ratio of rapid approaches.

5.525 Type of Withdrawal

By definition chases mirror a rapid withdrawal and are therefore not included in the test of independence. The type of withdrawal was significantly dependent on give-ways and fights (Table 5.21a).

Give-ways were followed by approximately equal proportions of relaxed (.48) and rapid withdrawals (.52), whereas fights were followed by a significantly higher proportion of rapid withdrawals (.91) (Table 5.21b). Thus the more vigorous the interaction the greater the probability that it will be followed by a rapid withdrawal.

Although the dependence between sex of participants and type of withdrawal was not significant, there was a clear trend for interactions between participants of the same sex to have a higher frequency of rapid withdrawals than heterosexual interaction.

5.526 Place of Interactions

The type of interaction was significantly dependent on the site (Table 5.22a). Both give-ways and fights had a significantly higher proportion (.87 and .86 respectively) than chases if they occurred in trees (Table 5.22b). Also significantly dependent were the site of the interaction and the sex of the participants. Both categories of heterosexual interactions formed a homogeneous group, with a significantly higher proportion occurring in trees than interactions between participants of the same sex, who also formed a homogeneous group (Table 5.22c). However, if trees are divided into den trees and other trees, male-to-female interactions differ significantly from female-to-female interactions which have a higher proportion occurring in den trees (Table 5.23).

With no significant statistical "interaction" in Table 5.22a it follows that heterosexual give-ways and fights have the highest porportion occurring in trees, while chases between participants of the same sex have the highest proportion occurring on the ground.

5.527 Time of Interaction

Table 5.24

Observations of the type of interaction in relation to sex of participants and time of night. Only 1966 all night observations used.

A Time	B Sex of participants	C No. of observations Type of interactions Give-way	Chase	Fight	Total
Before midnight	Male-to-female	8	2	4	14
	Female-to-male	7	1	4	12
	Male-male	4	4	0	8
	Female-female	1	1	3	5
		20	8	11	39
After midnight	Male-to-female	13	2	7	22
	Female-to-male	4	5	6	15
	Male-male	4	4	1	9
	Female-female	4	4	0	8
		25	15	14	54
Total		45	23	25	93

Hypothesis tested		d.f.	G	P
A x B	independence	3	0.456	>.9
A x C	"	2	0.656	>.5
B x C	"	6	13.626	<.05+
A x B x C	interaction	6	12.024	<.05+
A x B x C	independence	17	26.762	<.05+

Table 5.25

a) Observations of the occurrence of screeches in relation to the type of interaction and sex of the participants.

A	B	C			
		No. of observations			
Sex of participants	Presence of screech	Type of interaction: Give-way	Chase	Fight	Total
Male-to-female	Present	35	4	18	57
	Absent	45	5	9	59
		80	9	27	116
Female-to-male	Present	14	5	8	27
	Absent	53	16	5	74
		67	21	13	101
Male-male	Present	0	3	5	8
	Absent	28	36	19	83
		28	39	24	91
Female-female	Present	1	3	1	5
	Absent	8	6	5	19
		9	9	6	24
Total		184	78	70	332
Total screeches	Present	50	15	32	97
	Absent	134	63	38	235

Hypothesis tested		d.f.	G	P
A x B	independence	3	44.320	<.005 +++
A x C	"	6	54.616	<.005 +++
B x C	"	2	12.942	<.005 +++
A x B x C	interaction	6	9.542	>.1
A x B x C	independence	17	121.420	<.005 +++

b) Partitioning : Screech x sex of participants

Screech (proportions)			G (level of significance, 1d.f.)		
Present	Absent		M-to-f	F-to-m	F-f
.49	.51	M-to-f	-		
.27	.73	F-to-m	11.616+++	-	
.21	.79	F-f	6.912+	0.366	-
.09	.91	M-m	42.872+++	10.890+++	2.432

c) Partitioning : Screech x interaction

Screech (proportions)			G (level of significance, 1d.f.)	
Present	Absent		Fight	Give-way
.46	.54	Fight	-	
.27	.73	Give-way	7.728++	-
.19	.81	Chase	6.055+	1.918

Table 5.26

a) Observations of the occurrence of grunts in relation to the type of interaction and sex of participants

A Sex of participant	B Presence of grunt	C No. of observations Type of interaction Give-way	Chase	Fight	Total
Male-to-female	Present	10	2	12	24
	Absent	70	7	15	92
		80	9	27	116
Female-to-male	Present	0	1	2	3
	Absent	67	20	11	98
		67	21	13	101
Male-male	Present	0	4	2	6
	Absent	28	35	22	85
		28	39	24	91
Female-female	Present	0	2	1	3
	Absent	9	7	5	21
		9	9	6	24
Total		184	78	70	332
Total Grunts	Present	10	9	17	36
	Absent	174	69	53	296

Hypothesis tested	d.f.	G	P
A x B independence	3	20.312	<.005+++
A x C "	6	54.616	<.005+++
B x C "	2	16.812	<.005+++
A x B x C interaction	6	10.158	>.1
A x B x C independence	17	101.898	<.005+++

b) Partitioning : Grunt x sex of participants

Grunt (proportions) Present	Absent		G (level of significance, 1d.f.) M-to-f	F-f	M-m
.21	.79	M-to-f	-		
.13	.87	F-f	0.934	-	
.07	.93	M-m	8.816+++	0.826	-
.03	.97	F-to-m	17.746+++	3.052	1.424

c) Partitioning : Grunt x interaction

Grunt (proportions) Present	Absent		G (level of significance, 1d.f.) Fight	Chase
.24	.76	Fight	-	
.12	.88	Chase	4.170+	-
.05	.95	Give-way	16.170+++	2.814

Table 5.27

a) Observation of the occurrence of chatters in relation to the type of interaction and sex of participants.

A Sex of participants	B Presence of Chatter	C No. of observations Type of interaction Give-way	Chase	Fight	Total
Male-to-female	Present	3	0	7	10
	Absent	77	9	20	106
		80	9	27	116
Female-to-male	Present	1	3	3	7
	Absent	66	18	10	94
		67	21	13	101
Male-male	Present	1	6	5	12
	Absent	27	33	19	79
		28	39	24	91
Female-female	Present	0	2	0	2
	Absent	9	7	6	22
		9	9	6	24
Total		184	78	70	332
Total Chatters	Present	5	11	15	31
	Absent	179	67	55	301

Hypothesis tested		d.f.	G	P
A x B	independence	3	2.286	>.1
A x C	"	6	54.616	<.005+++
B x C	"	2	23.898	<.005+++
A x B x C	interaction	6	5.472	>.1
A x B x C	independence	17	86.272	<.005+++

b) Partitioning : Chatter x interaction

Chatter (proportions) Present	Absent		G (level of significance, 1d.f.) Fight	Chase
.21	.79	Fight	-	
.14	.86	Chase	1.364	-
.03	.97	Give-way	21.386+	11.084+

Interactions were tested for independence according to whether they took place before or after midnight. Neither the type of interaction nor the sex of the participants showed any significant dependence on time (Table 5.24).

5.528 Vocalisations

The screech was the most common call with a significant dependence both on the type of interaction and the sex of participants (Table 5.25a). Male-to-female interactions have the highest proportion of interactions with screeches (.49), differing significantly from all other combinations, and male-male have the lowest (.09) (Table 5.25b). Fights have a significantly higher proportion of interactions with a screech (.46) than both give-ways (.27) and chases (.19) (Table 5.25c). With an insignificant statistical "interaction" it follows that male-to-female fights are the noisiest, whereas chases between participants of the same sex are the quietest.

Grunts were also significantly dependent on the sex of the participants and the type of interaction (Table 5.26a). Male-to-female interactions had the highest proportion with grunts (.21) differing significantly from both male-male and female-to-female interactions, and female-to-male had the lowest (.03) (Table 5.26b).

Fights were significantly more often accompanied by grunts than both chases and give-ways (Table 5.26c). With an insignificant statistical "interaction" it follows that male-to-female fights are the interactions most frequently accompanied by grunts, and for female-to-male give-ways to be least frequently accompanied by grunts.

Chatters showed a significant dependence with the type of interaction but not the sex of participants (Table 5.27a), with a significantly lower proportion of give-ways (.03) being accompanied by chatters than both chases (.14) and fights (.21)(Table 5.27b).

5.53 Spacing of individuals following an interaction

Interactions in which the participants stay close together following an interaction, are assumed to be primarily concerned with the maintenance of individual distance, whereas those in which a participant leaves the

Table 5.23

a) Observations of spacing between individuals (see text for categories) subsequent to an agonistic interaction in relation to sex of participants and type of interaction.

A Sex of participants	B Type of Interaction	C No. of observations Subsequent spacing "Separate"	"Remain"	"Leave"	Total
Male-to-female	Give-way	73	10	8	91
	Chase	7	3	0	10
	Fight	20	4	2	26
		100	17	10	127
Female-to-male	Give-way	51	12	7	70
	Chase	12	9	0	21
	Fight	4	7	2	13
		67	28	9	104
Male-male	Give-way	13	14	3	30
	Chase	22	7	5	34
	Fight	12	7	4	23
		47	28	12	87
Female-female	Give-way	1	3	4	8
	Chase	0	1	6	7
	Fight	1	1	3	5
		2	5	13	20
Total		216	78	44	338

Hypothesis tested	d.f.	G	P
A x B independence	6	47.523	<.005 +++
A x C "	6	54.957	<.005 +++
B x C "	4	6.231	>.1
A x B x C interaction	12	21.452	<.05 +
A x B x C independence	28	130.364	<.005 +++

b) Partitioning : spacing x sex

Spacing (proportions) "Separate"	"Remain"	"Leave"		G (Level of significance, d.f.) M-to-f	F-to-m	M-m
.79	.13	.08	M-to-f	-		
.64	.27	.09	F-to-m	7.039+	-	
.54	.32	.14	M-m	14.924+++	2.442	-
.10	.25	.65	F-f	42.172+++	33.623+++	23.687+++

Table 5.29

a) Observations of spacing between individuals subsequent to an agonistic interaction in relation to sex of participants and site of interaction.

A Site of interaction	B Sex of participants	C No. of observations Subsequent spacing "Separate"	"Remain"	"Leave"	Total
Den tree	Male-to-female	43	8	7	58
	Female-to-male	35	21	7	63
	Male-male	10	10	1	21
	Female-female	0	2	5	7
		88	41	20	149
Other tree	Male-to-female	46	7	2	55
	Female-to-male	29	5	2	36
	Male-male	27	8	7	42
	Female-female	0	3	0	3
		102	23	11	136
Ground	Male-to-female	11	4	1	16
	Female-to-male	3	1	1	5
	Male-male	10	10	4	24
	Female-female	3	0	7	10
		27	15	13	55
Total		217	79	44	340

Hypothesis tested		d.f.	G	P
A x B	independence	6	49.646	.005+++
A x C	"	4	15.941	.005+++
B x C	"	6	45.573	.005+++
A x B x C interaction		12	20.861	.05 +
A x B x C independence		28	132.021	.005+++

b) Partitioning : spacing x site

spacing (proportions) "Separate"	"Remain"	"Leave"		G (level of significance, 2d.f.) Ground	Den tree
.49	.27	.24	Ground	-	
.59	.28	.13	Den tree	3.126	-
.75	.17	.08	Other tree	12.872+++	8.219+

vicinity of the other have a higher territorial component.

Three categories of subsequent spacing are recognised. Participants (1) "separate", if they remain in obvious social contact and remain within 3m of each other, or if at least one participant continues to show overt interest in the other; (2) "remain", in vicinity of each other if they move more than 3m, but less than 20m apart and take no further overt interest in each other, or remain in the same tree; (3) "leave", the vicinity of each other if one leaves the tree, or moves more than 20m away on the ground. Although 20m is an arbitrary distance chosen, in fact when a possum left the vicinity of another it usually continued to move much further away and had obviously broken off immediate social contact.

Subsequent spacing was dependent on the sex of the participants, but not on the type of interaction (Table 5.28a). Male-to-female interactions have the highest proportion of "separate" (.79), differing significantly from all other categories (Table 5.28b), thus it is assumed that they are primarily concerned with individual spacing. The female-to-male interactions have a higher territorial component (mainly "remain") which is probably the result of aggressive interactions over dens. Male-male interactions, though differing significantly from male-to-female, still have a remarkably high proportion of "separate". This is attributed to the fact that most interactions took place in the vicinity of an oestrous female, and both males remain close to her. The highest territorial component is amongst females who have a high proportion of "leave" (.65), and the "remain" proportion (.25) possibly represents interactions concerned with an individual distance greater than in other categories of participants.

A significant dependence also occurred between the locality of the interaction and the subsequent spacing (Table 5.29a). Interactions taking place in a tree, other than a den tree, differed significantly from both ground and den tree interactions and had a higher proportion in which individuals merely separated. This is consistent with the argument that den trees are territorial focal points.

5.54 Conclusions

Table 5.30

Summary of significant differences between sex of participants obtained from partitioning in factors where there was a significant dependence on the sex of the participants (see Tables 5.14 to 5.29). 1, 2 and 3 asterisks indicate significant probability levels of independence less than 0.5, 0.01 and 0.005 respectively. 0 = no significant difference.

	Months with conceptions	Place	Subsequent spacing	Grunt	Screech	Approach	Chase length	Fight + chase	Fight	Interactions (total)	No. of significant differences	
Female-to-male	0	*	0	***	***	0	0	0	0	***	4	Male-to-female
Male-male	0	0	***	***	***	*	*	***	***	***	8	Male-to-female
	**	***	0	0	***	*	*	*	*	***	8	Female-to-male
Female-female	0	***	***	0	*	*	0	0	***	***	6	Male-to-female
	0	***	***	0	0	*	0	0	***	*	5	Female-to-male
	*	0	***	0	0	0	0	0	***	0	3	Male-male

The significant differences between the four categories of participants are summarised in Table 5.30 for those factors which were significantly dependent with the sex of the participants.

Male-to-female interactions are the mildest, with the highest proportion of give-ways, relaxed approaches, low intensity fights and short chases, and the lowest proportion of chases following a fight. The high proportion of screeches and grunts indicate a high threat component, and it is argued that interactions, especially fights, are less serious. Male-to-female fights have a high proportion of wrestles, possibly due to the female's increased sexual attraction which overrides the male's tendency to retreat, and leads to a fight if the female is not ready to mate.

Female-to-male interactions differed significantly from male-to-female interactions in that there was a higher proportion of chases and rump fights, and a lower proportion of screeches and grunts. This suggests that when it is the female who approaches, the male withdraws, often rapidly, and without any initial threat. The significantly higher proportion of interactions occurring in den trees is attributed to competition for dens.

Male-male interactions are more overtly aggressive, with a higher proportion of vigorous or long fights, chases following fights, and rapid approaches. The lower proportion of screeches in comparison to heterosexual interactions is also interpreted as an indication of a more overt aggression. Fights in particular contained very little vocal threat and appeared to be more concerned with actual biting.

Female-female interactions resemble male-male interactions more closely than heterosexual interactions (Table 5.30), except that fights were almost exclusively of the leaping type, had a significantly higher territorial component, and were not affected by the months of conception.

That the sex of the participants has a significant influence on the ratio of the types of interactions and associated behaviours is evident from the foregoing tests of independence. Other "interactions" not tested

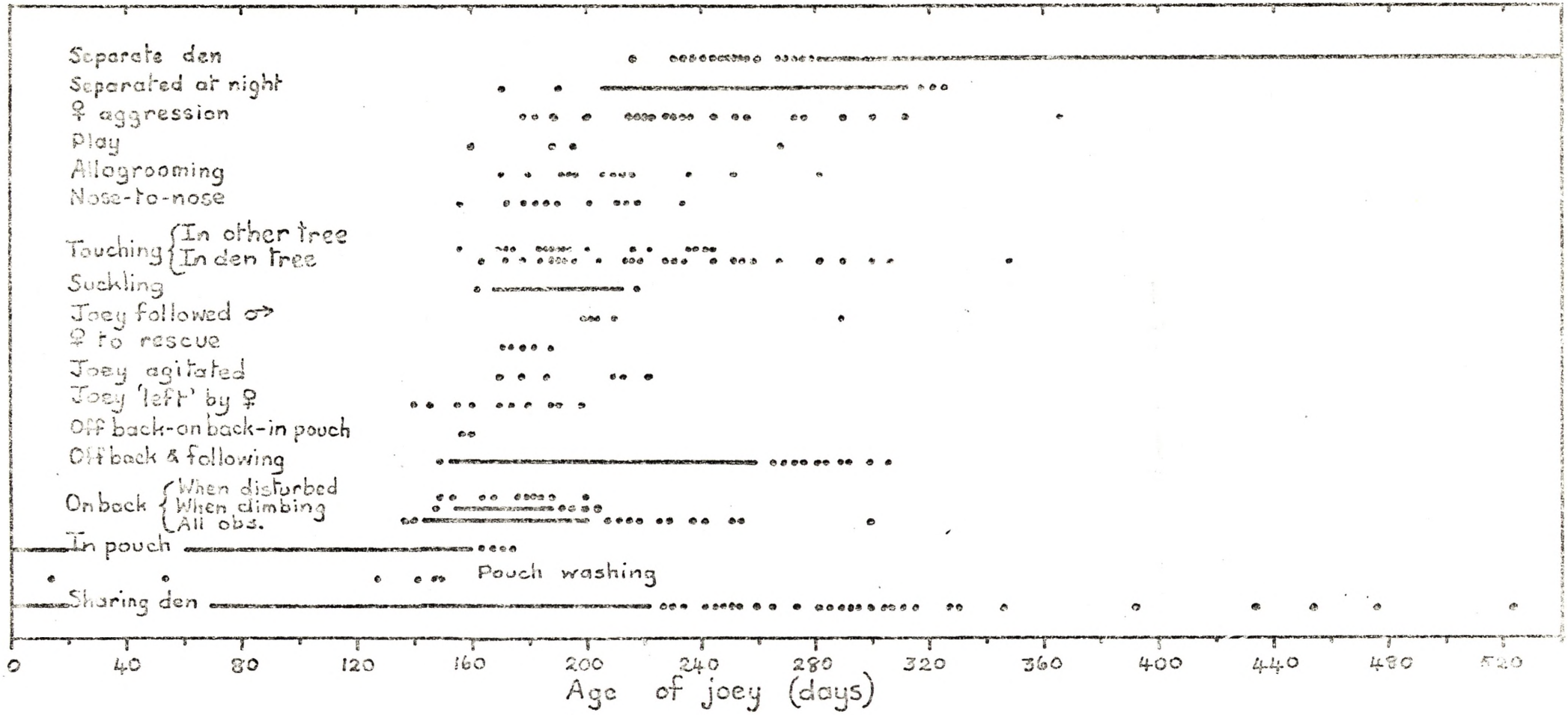


Figure 5.16 : Observations of mother-joey behaviour, in relation to age of joey. Dots = individual obs, continuous line = numerous obs.

for any social contact between the various tribes, but they do not offset the general conclusions.

5.6 ADULT FEMALE-JUVENILE RELATIONSHIPS

5.61 Mother-Joey Relations

5.611 Introduction

The first social contact between a mother and her offspring is at birth. In the marsupial this occurs at a very early age in the development of the young (virtually at the embryonic stage) when it makes the journey from the cloaca to the pouch. This is then followed by a comparatively long pouch life.

The only help the mother gives to her young as it makes its way to the pouch is to lie back on her haunches, which prevents the climbing 'embryo' from falling to the ground. She does not hold open the pouch, or retrieve the young one if it falls, and any licking of the fur is done after the young has reached the safety of the pouch (Lyne, Pilton and Sharman 1959).

5.612 Pouch Life

A few incidental observations were made on potential social interactions while the joey was confined to the pouch. These were limited to the female grooming the inside of her pouch and/or the joey. When doing this the female sat upright with the pouch protruding in front of her, and buried her nose in the pouch. Her front legs hung loosely down each side of the bulging pouch or gripped the fur of the abdomen. Once the female was seen to hold the pouch open with her front paws as she washed the inside. Another time the pink skinned body of the 53 day old joey could be seen half out of the pouch as its mother licked it.

All six observations were made at night when the female was away from her den and tended to be clustered towards the end of the joey's pouch life (Fig. 5.16) at ages 12, 53, 127, 141, 148 and 149 days respectively. Undoubtedly most pouch grooming and other possible social interactions between the mother and her pouch young occur in the den during the day.

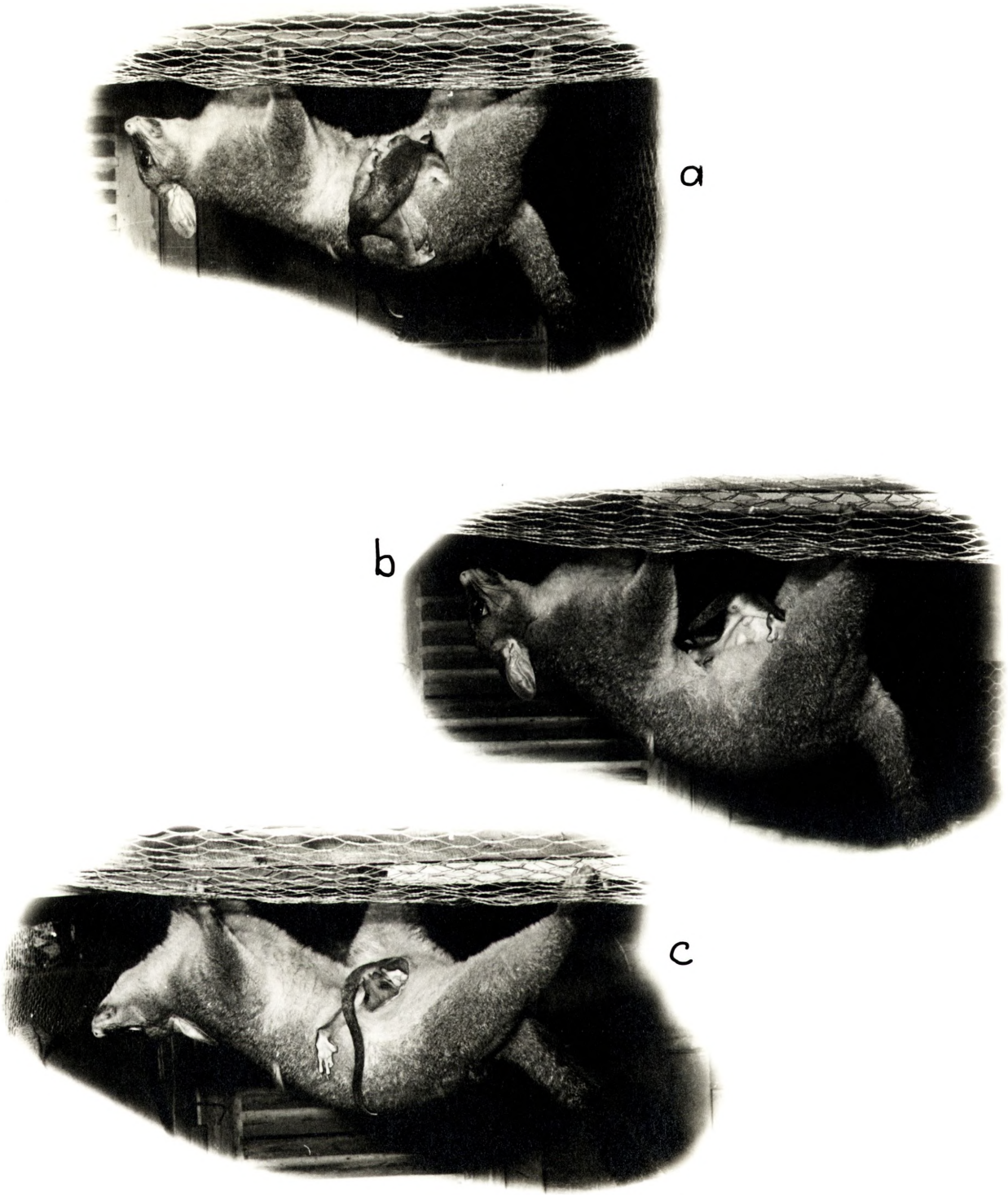


Figure 5.17 : Joey (4 months old) entering pouch of mother who is hanging upside down. Note somersault performed by joey.

Figure 5.18 : Mother carrying 4 month old joey in pouch. Note joey's front paw protruding from pouch opening.

5.613 Transition from Pouch Life to Independence

5.6131 Pouch Life to Back Riding

A young possum first comes out of the pouch during the day when its mother is in her den. In the field the earliest indication of this is the sight of a small short furred joey, with long gangling limbs, clinging to its mother as she emerges from her den at dusk, and with the joey making determined efforts to enter the pouch.

The pouch of the brush-tail possum has an anterior opening, and to enter it the joey needed to be clinging to its mother's flank in a transverse position with its head directed at the pouch opening, or in a more longitudinal position facing backwards. Occasionally if the female was sitting or standing on an horizontal branch the joey lay on its back on the branch with its head in the pouch region, hindquarters between the female's front legs, and its hind feet either gripping the female's neck or waving about as it attempted to find a foothold.

To enter the pouch the joey first pushes its nose into the opening, sometimes with a side to side motion obviously in an effort to open the pouch which can be closed by a sphincter muscle. A joey was never seen to use its front paws to initially open the pouch, but once the joey has its head buried in the pouch then the forepaws widened the opening. With much pushing and scrambling the joey manages to get first its forelimbs and shoulders, then its hind limbs and rump into the pouch. Although it may perform a somersault in the pouch as it enters (Fig. 5.17), there appeared to be no attempt to position its nose near the pouch opening, and Dolley and Dunnet (1960) have shown a joey can withstand relatively high concentrations of CO_2. If any part of the joey was left protruding from the pouch it was its rump, tail, or a limb (Fig. 5.18). Even towards the end of its pouch life the joey did not ride with its head protruding as is commonly the case in macropods (Sharman & Calaby 1964, Russell 1970b, Kaufmann 1974).

A mother's only assistance to her joey as it made efforts to enter the pouch was to stand still and possibly to make the pouch more accessable by standing with her hind legs apart. An example of this is given in

the following protocol.,

30.8.68 "19.01.....joey hanging onto the flank of the female facing back and partly underneath, but not right under the belly, and is nosing about in the pouch region. 19.02 the female is in what looks to be rather an awkward position with her legs spread out to different branches so that she is in a spreadeagled position. She may have taken up this position to make it easier for the joey to get at her pouch. The joey now underneath her upside down facing back, head in pouch region, and clinging to mother's belly, its hind legs hanging onto her neck. Tail? Mother sitting motionless in the spread-eagled position, not feeding and not looking at me. Joey lost its grip with its hind legs and there was a bit of a scramble, mother looked down and moved one front paw, but apparently not to steady the joey. Joey pushing vigorously at the pouch, now with head right in and back and tail still out, then mother moved along the branch a little. 19.05 joey half in pouch, mother sitting looking at me. 19.06 joey has managed to scramble further into pouch and only rump and tail showing, pouch gaping 3-4 inches, but joey definitely inside it. Mother just sitting looking in my direction."

In the above observation the female apparently took up the spread-eagled position to allow her joey to enter the pouch and maintained it until the joey was at least half in the pouch. The joey had made two previous attempts to enter the pouch, each time unsuccessful and in each the female remained sitting in a crouched position with its legs tucked under her body. In the first more vigorous attempt as the joey was pushing at the pouch opening the female kept moving a hind foot up and down, with it sometimes resting on the joey. However, it did not look like a deliberate attempt on the part of the female to push her joey away from the pouch, and may have been an avoidance reaction to the joey which kept licking its mother's hind foot. Another female was observed squatting on a branch, one hind foot in front of the other, her knees well apart, and front feet well forward and one up on a small twig, as her joey struggled to enter the pouch.

A female was never observed to assist her joey to enter the pouch by nuzzling, pulling, pushing, or by holding the pouch open.

Conversely, a female's only action to stop her joey entering the pouch was to stand or sit in such a way that the joey either could not reach the pouch or could not enter even it it could reach the opening. Another means she had of discouraging, if not actually preventing, the joey from entering the pouch, was to keep walking. It is not known to what extent the female

Table 5.31

Observations of time spent out of pouch by joey at night

Age of joey in days	Time out of pouch not shorter than hr	min	not longer than hr	min	Remarks
138		10	6	47	
146		0		11	
146		19	1	49	
147		34	1	44	In pouch for rest of night
148		7		13	" " " " " "
148		11		15	" " " " " "
148		24	3	31	" " " " " "
151		48		50	
154		30	3	18	
156		?	1	28	
157	1	5	2	26	
158	2	38	2	38	
162	2	7	2	13	
170		0		7	On back again within 1hr 10 min

could prevent the joey from entering the pouch by constricting the pouch sphincter muscle, but this seems unlikely as at this stage the muscle is rather slack.

The time taken for a joey to enter the pouch from the time it had pushed its nose into the pouch opening until its hindquarters were in, was normally about 4 to 5 minutes. The longest time for any one continuous attempt, eventually successful, was 14 minutes, the most difficult part apparently being to get the hind feet into the pouch. Throughout this long bout the female remained sitting in one place.

If a joey was going to enter its mother's pouch it did so in the early part of the night. From the time of emerging from the den, 7 minutes was the shortest time that a joey was seen to be out of the pouch (Table 5.31), and the longest time was more than 2 hrs 38 min but less than 6 hrs 47 min, with 2.5 to 3 hrs probably being close to the true figure.

A joey leaves its mother's pouch in the den during the day, and when it enters the pouch after its mother has left her den it remains in it for the rest of the night. Only once was a joey seen out of the pouch after it had been observed in the pouch earlier in the night. It was also the oldest joey seen to enter the pouch after the female had left her den (Table 5.31). In all 4 observations in which a joey, after it had entered the pouch, was known to remain in it for the rest of the night the joeys were aged either 147 or 148 days (Table 5.31). The closeness of the ages was probably a coincidence rather than an indication that after 148 days joeys will come out of the pouch again later in the night. In one observation this happened in the 170 day old joey. Three observations support the contention that older joeys tend to stay in the pouch once they have entered it. One was of a 157 day old joey seen in the pouch at 03.53, another of a 162 day old joey observed in its mother's pouch from 02.08 until the female entered her den, and the third of a 166 day old joey in the pouch from 01.45 until entering the den.

The youngest joey seen out of the pouch in the field was 136 days,

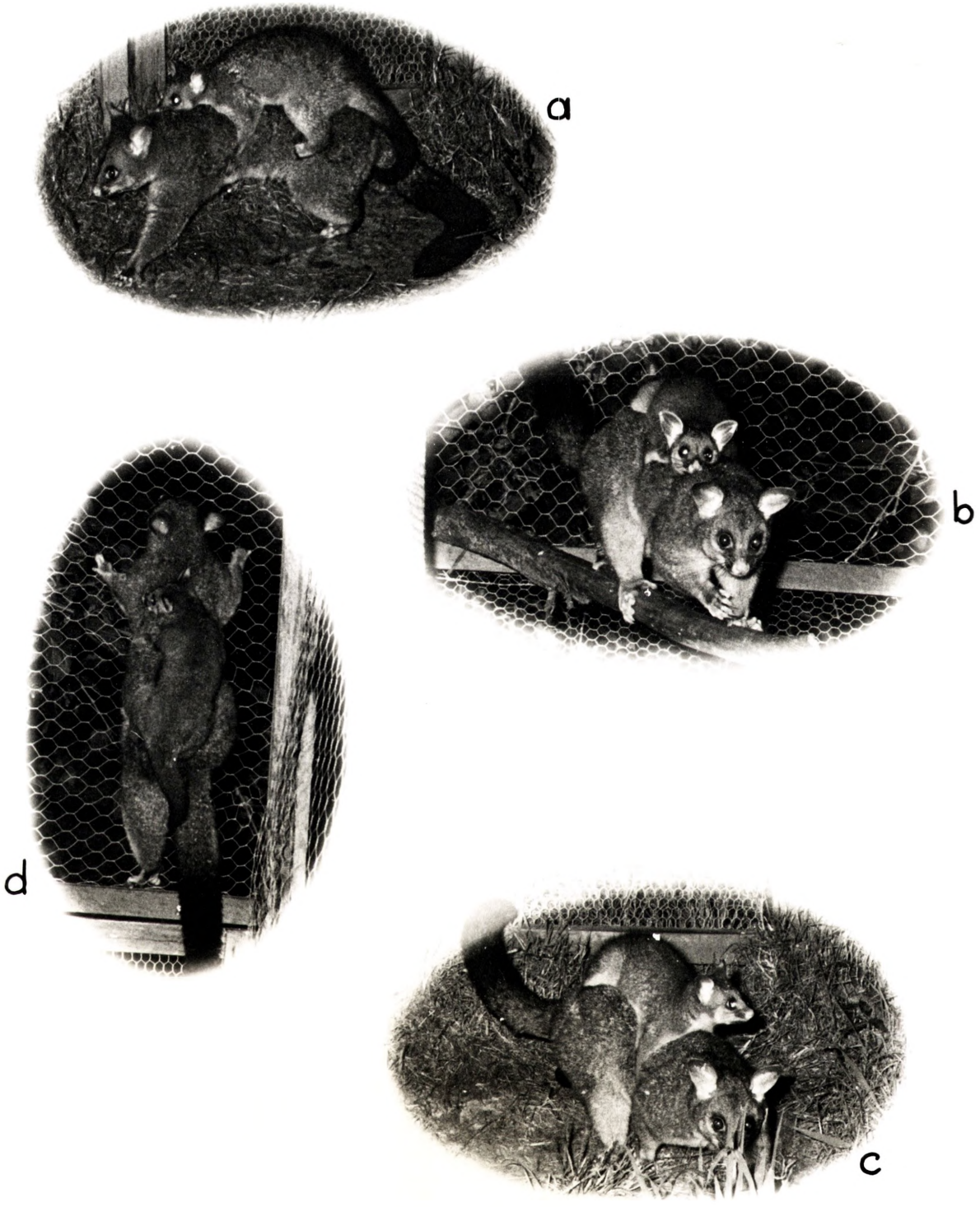


Figure 5.19 : Joey riding on mother's back. a and b, typical longitudinal facing forward position with chin pressed firmly on mother's back; c and d, head lifted off mother's back.

Table 5.33

The number of times a joey took up a variety of positions when riding on its mother during a 90 min observation period.

Age of Joey (days)	Types of Positions					
	Longitudinal facing forward	Longitudinal facing backward	Transverse	Head in pouch region	Under chin or belly	Diagonal
158	10	5	13	7	1	1
170	13	-	6	3	-	-
177	11	-	3	1	-	-
177	4	1	-	-	-	-
178	4	-	1	-	-	-
185	1	-	-	-	-	-
187	8	1	-	-	1	-
191	4	-	-	-	-	-
195	4	1	1	-	-	-
203	-	-	-	-	-	-
208	-	-	-	-	-	-
214	1	-	-	-	-	-
Total	60	8	24	11	2	1

and the oldest joey seen in the pouch was 173 days (Fig. 5.16), a time span of 37 days. The longest time span for this overlapping period for any one individual was 14 days, and with observations roughly once a week the first observation of a joey out of the pouch was often the last (Table 5.32). There was a sceptical case of a 199 day old joey in the pouch.

Table 5.32

Number of days between the first observation of a joey out of the pouch and the last observation in the pouch.

Age of joey (days)		Overlap (days)
First seen out of pouch	Last seen in pouch	
146	146	0
147	147	0
148	148	0
148	148	0
151	151	0
154	154	0
170	170	0
158	162	4
162	166	4
148	156	8
143	157	14

When first seen out of the pouch the joey clings tightly to its mother in more or less any position on her back, and shifted position frequently, sometimes facing forward, sometimes backward, sometimes transversally, over the female's back and even at times under the female's chin or between her hind legs. Most of these positions are related to the joeys' attempts to enter the pouch, but as the joey grows older and especially after it has ceased to enter the pouch it adopts the standard longitudinal facing forward position shown in Figure 5.19. This shift from a number of positions to the standard one is shown in Table 5.33.

In the longitudinal facing forward position the joey's front paws grip the mother's fur in the region of her arm pits, hind feet grip the fur on her hips, chin is pressed firmly down on her back between the shoulder blades, and the tail curled round the base of the female's tail (Fig. 5.19 a & b). Variations are numerous but not radically different. For instance the joey's tail may hang loosely to the side or rest on top of the female's tail; the joey may ride further back with

Figure 5.20 : Joey clinging to mother's fur when both hanging upside down. Note hold of joey's tail.

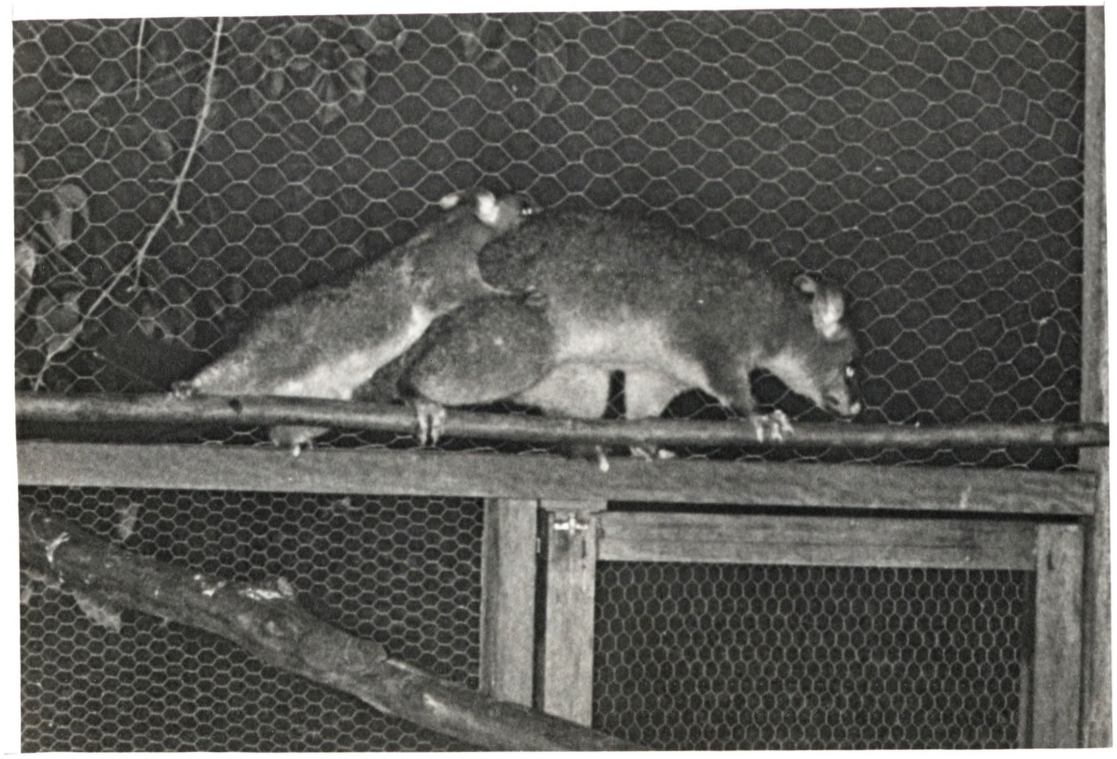


Figure 5.21 : Joey sliding backwards off mother's back as its mother moves forward.

its front paws gripping the female's flank in the lumbar region and the hind feet gripping each side of the tail; rarely was the joey well forward over its mother's shoulders except in the earlier stages of riding on her back.

As the joey gains confidence in riding on its mother's back it begins to lift its head away from the female's back, and takes more interest in its surroundings (Fig. 5.19 c & d). It will only assume the earlier position when disturbed or when the female is moving rapidly through a tree.

An indication that the joey clings to its mother by grasping handfuls of her fur, rather than by hugging her body is shown by Figure 5.20 where the joey can be seen hanging well away from its mother's body when she was upside down. Despite this the skin of the female's shoulders and hips become covered with small scratches whilst she is carrying a joey.

5.6132 Back Riding to Following

The next phase in the social development of the young possum is the breaking of bodily contact when it begins to get off its mother's back and move away from her. The earliest observation was at 148 days (Fig. 5.16).

Its first tentative forays are made when the female is stationary, in most cases while sitting on an horizontal branch. The joey clambered off to sit touching its mother, either immediately in front of, or behind her. It was the joey who took the initiative to dismount as, apart from sitting still, the female showed no signs of actively encouraging or forcing the joey to get off her back. In a third of the observations (Table 5.34) the female was moving forward as the joey got off her back. This it usually did by sliding off backwards over the female's rump (Fig. 5.21).

In some of these observations the timing of the female's movements appeared to be such that the joey was encouraged if not forced off her back. For example, when a 158 day old joey riding on its mother's back facing backwards reached out and grasped a twig the female quickly moved forward about 1m. The result whether intentional or not was that the joey, who continued to grasp the twig was pulled off her back. The joey did not

appear reluctant to leave its mother's back as it made no attempt to cling to her. In most observations however, it appeared as though the joey took advantage of the mother's forward movement to slide off backwards as indicated in the following protocols.

16.9.68 "17.48 Jill sitting on a branch, joey (170 days) on her back in longitudinal facing forward position. 19.50 both in same positions. 19.53 Jill moved down the branch very slowly and as she did so the joey slowly slid backwards over her rump and off her back over the base of the female's tail. Jill kept moving forward very slowly and did not stop until about 1 foot beyond where the joey got off."

6.10.68 "20.07 Female 6147 turned into the head down position and began to come down the tree again, joey (191 days) still in longitudinal facing forward position. Female coming down the tree, joey still clinging to her back though it is beginning to slide off backwards so that its hind legs are on the branch instead of each side of the base of the tail. The joey then slid off at 20.07 and is following about 1 foot behind its mother."

Table 5.34

Movements of female in relation to her joey climbing off or onto her back.

Joey climbing off		
Female		
Stationary		27
Moving forward - joey slid off backwards		12
- joey brushed off by branch		1
Total		40
Joey climbing on		
Female		
Stationary		17
Moving away		
Intention movement	3	
Without a pause	11	21
With a pause	7	
Moving towards		1
Total		39

A female was never seen to attempt to dislodge a joey by pulling or biting at it. Once a joey was pushed off its mother's back by a overhanging branch, and once a joey was squeezed off its mother's back when the female sat back in the fork of a branch. Neither of these appeared to be deliberate attempts by the female to dislodge her joey.

A joey when it first begins to get off its mother's back stays close to her, and with any movement of the female away, even an intention

movement, the joey immediately clambers onto its mother's back, to cling to her in the longitudinal facing forward position. If it climbs over the female's head the joey will turn to face forward once on her back, giving two to three kneading movements with its paws as it settles into position.

In a tree a joey typically follows 1 to 2m behind the female. However, it may wait until the female is further away than 2m before it starts to follow, and will then catch up at a run. Also the joey may come right up to the female so that its nose is level with the base of the female's tail, this is especially so when the female is climbing either up or down the branchless 4-5 metres of the bole of the tree above the ground. When coming down a tree the female frequently stops to sit on a branch and the joey will come to sit beside and touching her. Then, when the female continues her descent the joey will wait until the female has gone 2 to 3m before following. Only once or twice was a joey seen to travel ahead of its mother, other than in an agonistic interaction, and then only for about 3m.

On the ground a joey tends to keep closer to its mother than it does in a tree.. Generally a joey which has recently begun to follow its mother keeps about 0.6m from the tip of its mother's tail. If the female is travelling rapidly or if the joey is not watching its mother closely, it lags behind but when 2-3m (sometimes up to 6m) behind it will catch up with a few bounds. In the rush to catch up with its mother the joey typically comes within 0.3m of her, but quickly drops back to about 0.6m either by pausing or by actually turning and moving away. It appears that 0.6 to 1m is the optimum distance for the joey to follow its mother. It does not appear to be a socially imposed distance in the sense that coming closer illicites agonistic behaviour. This comes later. Older joeys (e.g. 281 days) who are still following their mothers will stray further away, up to about 10m for much of the time, but even they keep returning to her, though by this age agonistic behaviour has probably developed and will prevent the joey coming any closer than 1m (see Section 5.617).

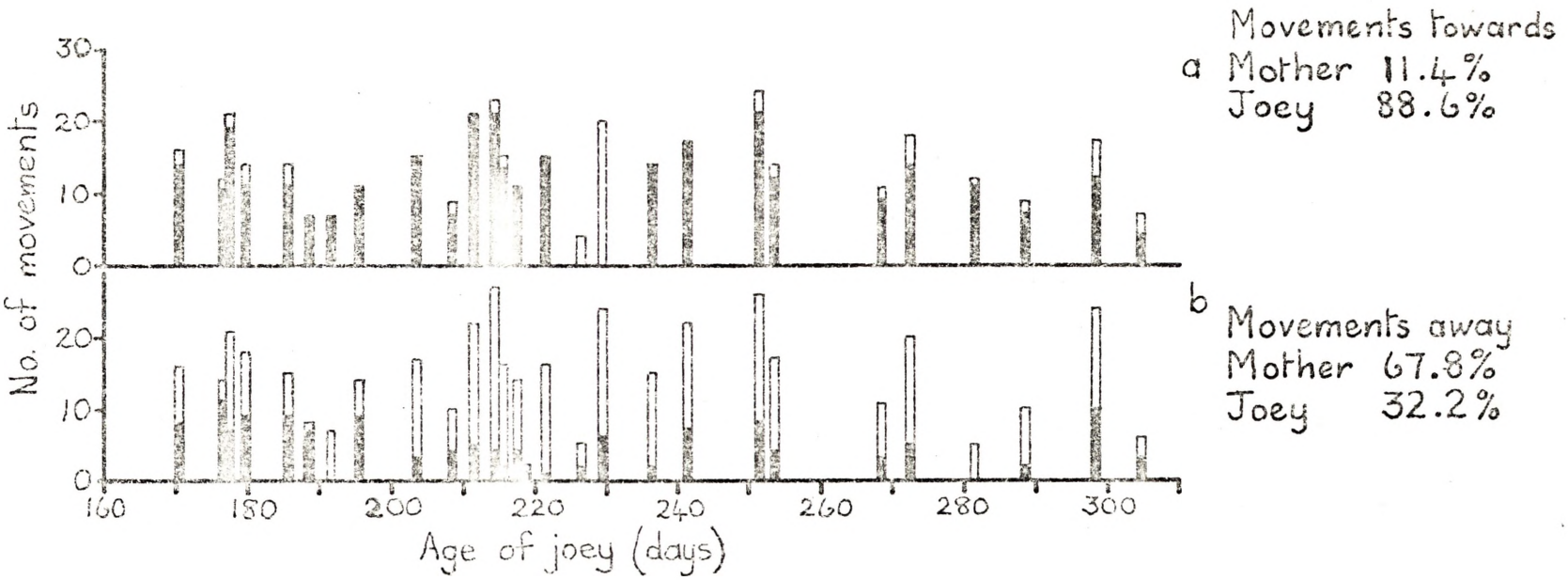


Figure 5.22 : Mother-joey movements relative to one another.
a) movements made towards the other individual,
b) movements made away. Solid column = movements by joey; open column = movements by mother.

When a female climbs a tree from the ground her joey who has been following within 1m of her may stay at the base of the tree until the female is 6 to 7m up it. It is as if the action of the female climbing the tree vertically did not represent a movement away from the joey, who behaved for a short while as though the distance from it to the tree base was the distance between it and its mother. On the other hand if the joey did follow its mother up the tree immediately it often kept its nose level with the base of the female's tail.

I could not detect any signal, auditory or visual, given by the female that she was about to move away and that the joey should either climb onto her back or follow. In the early phase when the joey had just begun to get off its mother's back, any movement made it climb back on. Later the female could move slowly away from the joey without the joey making any attempt to follow. However, should the female move away rapidly at a steady pace the joey would follow. To move away rapidly may therefore be the cue given by the female to her joey to follow but one that has not evolved to the level of a signal.

In a third of the observations in which a joey climbed onto its mother's back after the female had begun to move away, the female made a distinct pause after she had travelled 2 to 3m (Table 5.34). This allowed the joey to catch up with her and to climb onto her back. The steady walking away and the distinct pause was the limit of the female's cues to her joey. The female does not move towards her joey before moving away as only 11.4% of all movements, made by either the joey or the female towards the other, were by the female (Fig. 5.22). The few movements that she did make towards her joey tended to occur during random feeding movements. Also most (67.8%) of the movements made away from each other were made by the female (Fig. 5.22). A higher proportion of this type of movement was made by the joey, but occurred either when the female was sitting and the joey made exploratory sallies away from its mother, or when feeding.

In general therefore the onus of maintaining proximity rests with the joey. The mother gives no definite signal that she is about to move

away, and her cue of walking away rapidly, with or without a pause, depends on the joey keeping alert for such movements. Even at a very early age the responsibility lies with the joey, as indicated by the lack of any significant change in the proportion of movements of the female relative to her joey with respect to age of the joey (Fig. 5.22).

A joey may not be immediately aware of its mother's departure thus there may be a distinct lag before the joey does follow. When this occurs the joey suddenly realises that its mother has departed and rushes after her as in the following protocol.

9.10.65 "03.25 joey (188 days old) is now the other side of Gert and within 2ft. 03.30 Gert managed to cross to Mt6 (she had been making repeated attempts since 01.20), her joey feeding 2-3 feet behind her. Gert seemed to give no indication to the joey that she was going to move. Joey made no attempt to follow until the branch swung upwards when Gert's weight came off it. Joey then scrambled hurriedly along the branch, and luckily was able to cross the gap easily because it had closed with Gert's shift from one branch to the other. It ran quickly down the branch to join its mother, and stayed close to her."

If a joey did become more than momentarily separated from its mother it became agitated. This invariably occurred when the joey was unable to follow its mother across a gap. The joey frantically tried to reach across the gap and on failing to do so, ran up and down the branches looking for an alternative route, but frequently returning to the mother's crossing point. Six observations were made of joeys unable to follow their mother. In three of these observations typical agitated behaviour was shown by young joeys (169, 177, and 185 days old respectively). In all three the female showed no overt concern at her joey's agitation, but she apparently responded by not moving away from the vicinity. In one the female was coming down the tree when her 185 day old joey became separated and agitated. The female stopped head down on a diagonal branch, without looking back up at her joey. When, after 2-3 min, the joey found an alternative route, it clambered onto its mother's back from behind and the female continued her descent. In another the female moved 3-4m below where the joey (177 days old) had been unable to cross and fed for 9 mins, once moving back within 1m of the gap. Meanwhile her joey

behaved in an agitated manner, and frequently returned to the gap which it was unable to cross. Finally it approached a male and almost immediately its mother rapidly returned to her joey by a circuitous route. Both observations suggest that the females were aware of their joey's plight. The first one reacted by waiting, the second by staying close to the gap and by quickly rejoining her joey when it approached a male. In the third observation the 169 day old joey was prevented from taking a short alternative route by the presence of a male. After 5 mins the male moved, but instead of taking the opportunity to reach its mother the joey returned to their den nearby. Although the female appeared to ignore her joey she had moved only 3-4m from the gap in order to investigate a den. The oldest joey seen to become agitated at being separated from its mother was 220 days (Fig. 5.16). It had crossed a gap ahead of its mother, who turned back before reaching the gap, and the joey became very agitated when it was unable to recross the gap. At first the female stopped only 3m from the gap, but appeared to ignore her joey and soon moved to the other side of the tree. Usually by this age a joey was sufficiently familiar with its surroundings to quickly find an alternative route even if this meant coming down onto the ground. Twice when joeys (208 and 211 days old) were unable to follow their mothers across a gap, they unhesitatingly climbed rapidly down the tree, bounded across the ground and up the adjacent tree to their mother, and in one case the gap was 18-20m from the ground.

In another observation Jill appeared completely indifferent when her 208 day old joey followed a male out of the den tree and climbed into another about 52m away. However, when she left the den tree herself half an hour later, she rejoined her joey, possibly a coincidence but it appeared deliberate.

A joey of the Tyne St. Female was once observed to be very agitated, running about on the roof of the house, and giving zook-zook calls as it searched for its mother. These calls were not heard from the agitated joeys at Moggill Farm, but with a carrying distance of only 10-15m they

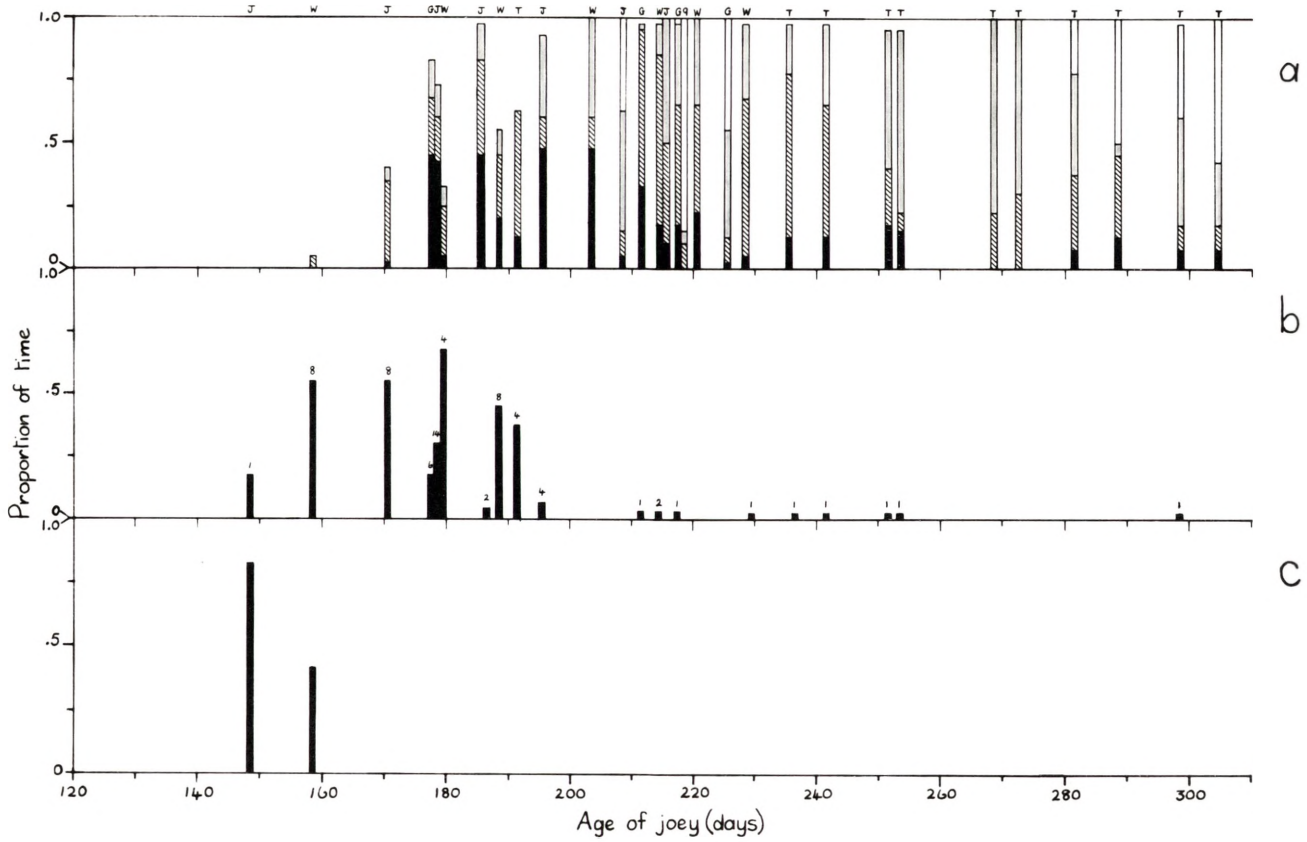


Figure 5.23: Proportion of time spent by the joey - a) off mother's back, black shading = touching, cross hatching = within 1m when following, grey shading = no closer than 1m when following, unshaded = travelling independently; b) on mother's back, figures = no. of times joey climbed onto mother's back; c) in pouch. Observations confined to first 90 mins after emerging from den at dusk.

could easily have been missed.

5.6133 Time Spent on Mother's Back

The youngest joey seen on its mother's back was 136 days old and the oldest 298 days, giving a time span of 162 days (Fig. 5.16). The longest time span for any one individual was 136 days, but this was unusual and a span of 50 to 70 days is probably average (Table 5.35), occurring between the age of about 140 to 210 days.

Table 5.35

Number of days between the first and last observation of a joey on its mother's back.

Age of joey (days) First seen on back	Last seen on back	Overlap (days)
187	195	8
190	198	8
164	173	9
151	164	13
139	153	14
147	167	20
160	181	21
154	176	22
171	193	22
164	187	23
146	172	26
166	194	28
158	187	29
170	199	29
162	195	33
164	198	34
148	186	38
148	188	40
136	187	51
147	198	51
148	199	51
154	206	52
148	211	63
143	210	67
158	229	71
162	298	136

An indication of the proportion of time spent on its mother's back is shown in Figure 5.23, and it decreases markedly after about 190 days. Up to 190 days the joey will climb onto its mother's back and stay on it for more than a minute, but older joeys do little more than get on then off again immediately.

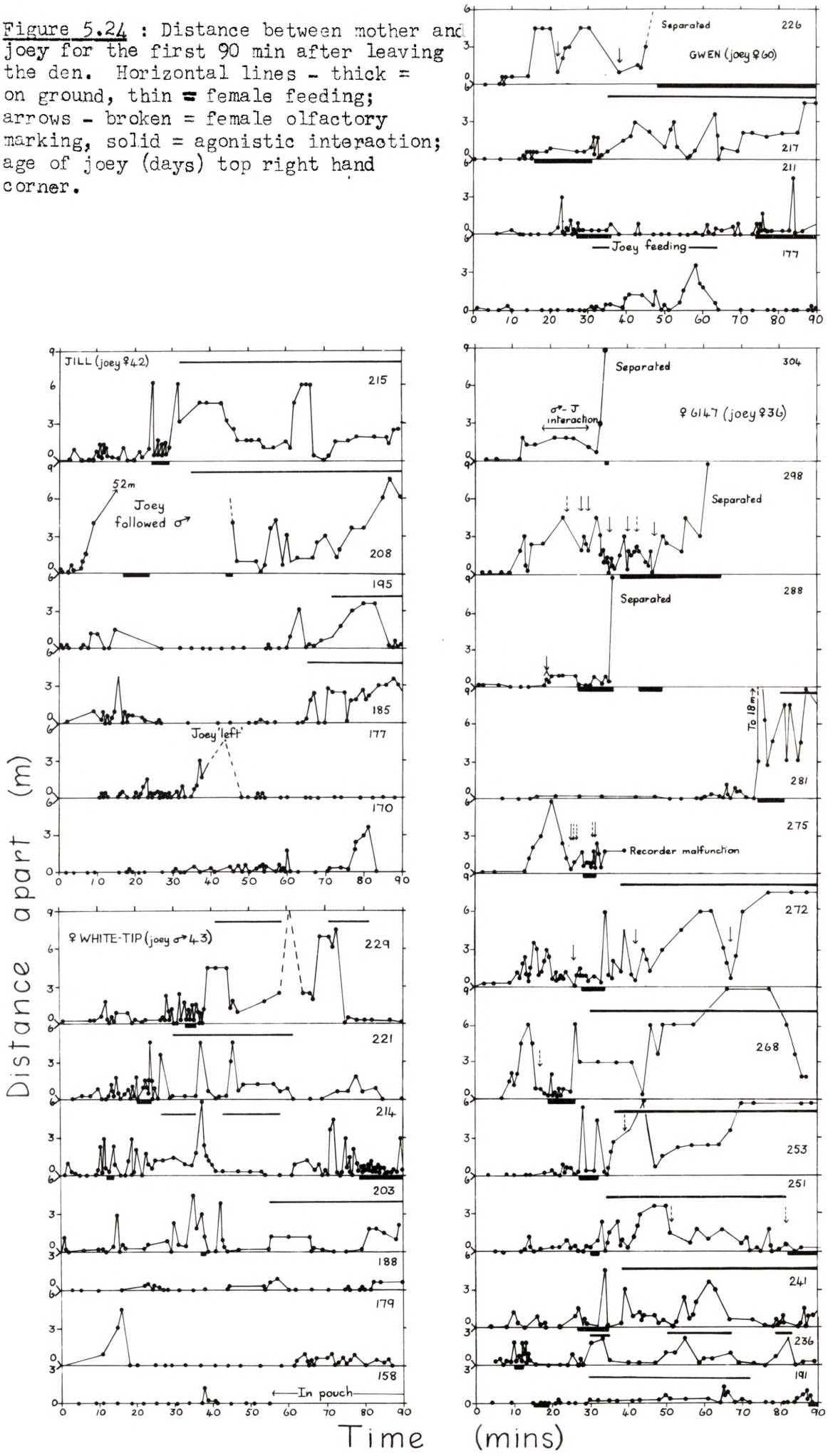
Even after a joey has begun to follow its mother rather than to

ride on her back it may climb onto her back for brief periods, usually less than 1 minute. These appear to function as a type of reassurance behaviour to the joey. For example Jill's 177 day old joey climbed onto her back 14 times in the first 90 min after emerging from the den tree, an unusually high frequency (Fig. 5.23), attributed to the presence of a male courting the joey's mother, making the joey unusually nervous. When feeding on the ground with its mother the two may stray apart, but at intervals the joey will return to its mother and may even climb onto her back briefly. Also up to the age of 199 days joeys were observed to climb onto their mother's back when disturbed by the spotlight or by my approach (Fig. 5.16). The oldest joey seen riding on its mother's back as she climbed into a tree was 198 days, and out of a tree 206 days (Fig. 5.16). This suggests that joeys cease to use backriding as a mode of transport at about this age, and thereafter it is predominantly for reassurance.

A feature of a possum's activity at night is that it may spend long periods just sitting in a tree, especially in the middle of the night. During these periods of inactivity a joey may climb onto its mother's back and remain very still for periods of up to 1.5 hrs. An example of this is the following behaviour of Alice's 187 day old joey throughout the night. When in the den tree the joey climbed onto its mother's back briefly once, and when feeding on the ground kept returning to her, actually climbing onto her back briefly three or four times. At 20.58 Alice settled down to sit on a branch. At first her joey sat 3m below her, but within 1 min climbed onto her back and stayed there until the female moved away 1.5 hrs later.

Whilst sitting they both gazed in my direction and my presence 80m away may have been the reason for the joey climbing onto its mother's back. Nevertheless when feeding and following its mother the joey appeared unconcerned by my presence. Two hours later the female was again sitting with the joey on her back, but it was not known for how long. This was the last observation of the joey on its mother's back even though it kept

Figure 5.24 : Distance between mother and joey for the first 90 min after leaving the den. Horizontal lines - thick = on ground, thin = female feeding; arrows - broken = female olfactory marking, solid = agonistic interaction; age of joey (days) top right hand corner.



close to her for the rest of the night. In a second all night observation Jill sat on the same branch for about 3.75 hrs, resting most of the time. Her 168 day old joey was on her back when she climbed to the branch, but it soon dismounted and spent the next hour tucked underneath Jill. This was followed by 20-40 mins on its mother's back, a further 50 min touching, on the back again for less than 20 min, and finally 10-15 min touching before Jill moved away. During this time the joey was pressed hard against its mother when not actually on her back.

5.6134 Distance Between Mother and Joey

In its first tentative forays away from its mother a joey will keep within 1m of her, and frequently returns, to sit within 0.3m, often touching, or even to climb onto her back. Similarly, at an early age the joey makes every endeavour to keep within 1m of its mother when she moves away, but sometimes the distance may be greater for short periods. As the joey's confidence increases it ventures further than 1m from its mother, and does not attempt to keep within 1m when following. The new distance up to which a joey will venture and still apparently feel secure is in the order of 3m, with a maximum of about 5m which is approximately the maximum distance it can move from its mother yet remain in the same clump of foliage of a major branch of the eucalypt trees in the study area.

If the distances recorded between the mother and joey for the first 90 minutes after leaving the den is examined, two main trends are apparent (Fig 5.24). One trend is for the mother and joey to spend a greater proportion of time further apart as the joey grows older, and is still following her. This is shown for all four mothers under observation, Jill, Female White-tip, Female 6147 and Gwen (Fig. 5.24).

It is most clearly demonstrated in the records for Jill and White-tip where the early traces show that mother and joey spend over 85% of the time within 1m of each other, and the time spent further apart was usually because of untoward circumstances. For instance, Jill's 177 day old joey was unable to follow her across a gap and had to wait for her to return,

and Female White-tips's 179 day old joey remained at the den entrance for 16 mins before rushing to join its mother. As a joey grows older an increasing proportion of its time is spent more than 1m from its mother, and less time either on her back or sitting touching her (Fig. 5.23).

A second clear trend is for the joey to begin to move further away (up to 5m) from its mother, after a period of keeping within 1m of her. This is clearly shown in Figure 5.24 for several females and their joeys (Jill 185, 215; Female White-tip 229; and Female 6147, 251, 253, 281), and is apparent in several others. The general pattern is for the joey to stay within 1m of its mother for varying lengths of time after they have emerged from the den, before switching to the other phase in which it moved further apart. The change frequently coincided with the first major feeding period of the female which usually took place after they had left the den tree and climbed into a second. A typical trace of this pattern is that for Jill and her 215 day old joey (Fig. 5.24). For the first 24 min after emerging from the den the joey kept within 1.03m of its mother, some of the time sitting touching her. When Jill came down the den tree the joey followed closely but lagged 6m behind when Jill leapt to the ground and bounded away. The joey caught up with its mother and whilst on the ground the distance between them fluctuated between 0.5 and 2m. It again lagged 6m behind when Jill climbed into a tree and settled down to feed. The joey made no further attempt to come within 1m of its mother for another 40 min when it came right up to her and sat touching for less than 1 min. Similarly the traces for Female 6147 with her joey at 251 and 253 days (Fig. 5.24) show a clear correlation between feeding and her joey moving further from her. The fact that it was feeding which was the primary cause of this shift, and not leaving of the den tree by Jill and her 185 day old joey is indicated where they did not leave her den tree before settling down to feed and the very close correlation between the start of the feeding period to a marked change in the spacing of Jill and her joey (Fig. 5.24). In another observation the female did not settle

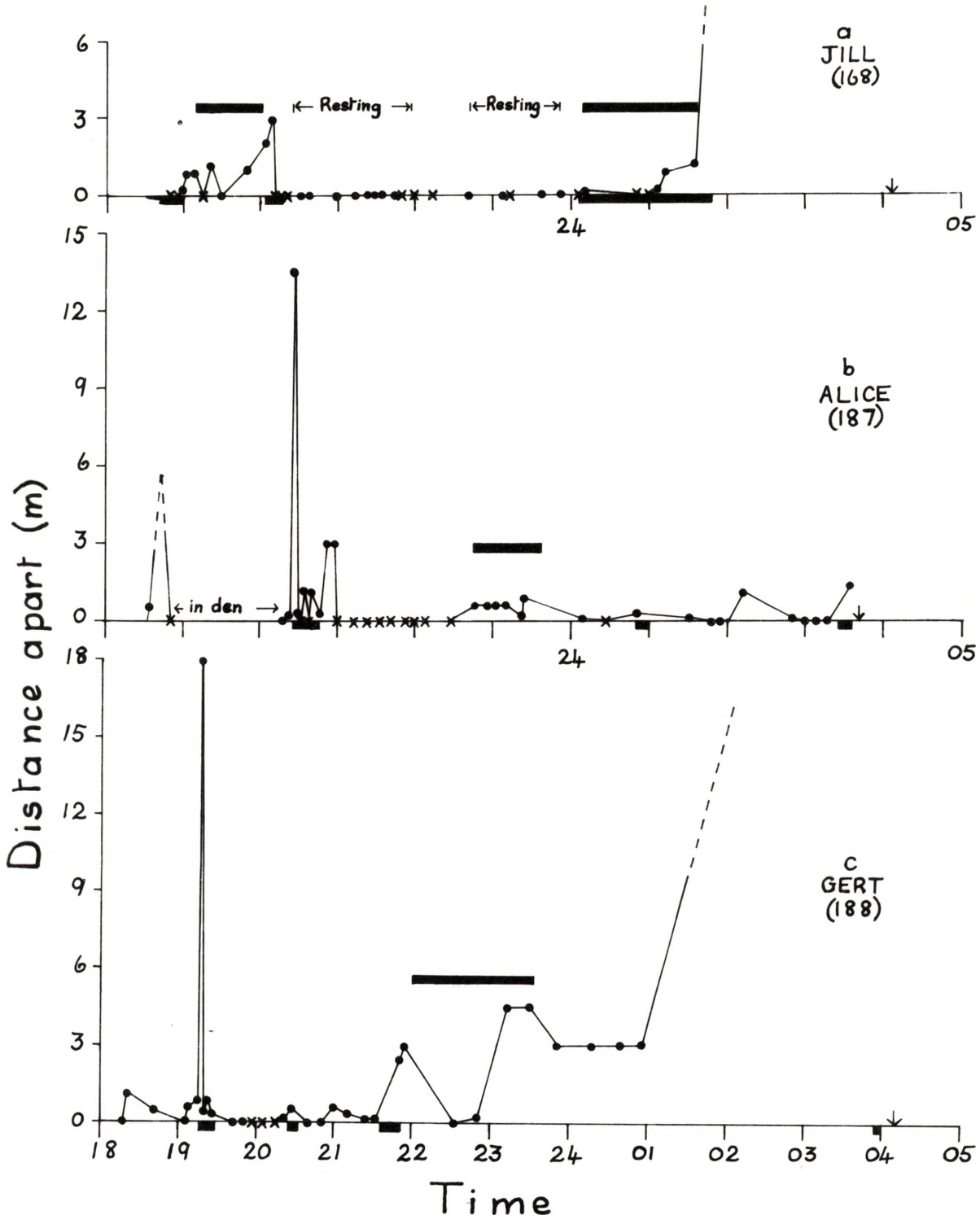


Figure 5.25 : Distance between mother and joey throughout the night. x = obs of joey on back; dot = obs off back; arrow = female into den; heavy horizontal lines - lower = female on ground, upper = female's main activity feeding; age of joey in days in brackets.

down to feed until she had climbed into a third tree after leaving her den tree, and her joey kept very close to her until she started to feed (Fig. 5.25c, Cert-188).

The probable explanation for this change in spatial relationships coinciding with the female settling down to feed lies in the joey's ability to predict its mother's movements. Before the female starts feeding in earnest she is likely to move off rapidly and to leave the tree she is in. Therefore the joey keeps close to her. She is less likely to do this once she starts to feed, thus giving the joey a chance to move away from her with a greatly reduced probability that its mother will move off without it being aware of it. This may also be the explanation why a joey will sit touching its mother or even get on her back when the female stops feeding and rests towards the middle of the night. Again the female is liable to leave the tree suddenly after resting, and if the joey is also resting it is less likely to lose contact with its mother if very close to her.

A female and her joey will drift apart as they feed, or even move into different clumps of vegetation, but from time to time the joey returns to its mother, coming within 1m or even right up to her (see Fig. 5.24. Jill, 203, 215; Female 6147, 241, 251; Female White-tip, 229, and Gwen, 217).

The following protocol gives one such approach by the joey, in which it sat touching its mother for less than 1 min.

31.10.68 "19.39 joey stopped feeding and came down to the trunk and up it 2 to 3 feet. It is still 20ft. from Jill. Joey grooming, Jill feeding. 19.40 joey is going up the branch. Jill is in the tree; joey now 10 ft, 8 ft from Jill and definitely moving towards her, 5 ft, 3 ft. 19.41 joey came within 1 ft of Jill who continued to feed. Joey started to feed 1 ft from Jill. 19.43 Joey has moved right up underneath Jill and is touching her, Jill reached over the Joey to feed. Both feeding and touching. 19.44 both feeding 1 ft apart. 19.46 Jill moved back along the branch away from the foliage clump, so about 5 ft. from the joey who continued to feed. Jill went along another branch and has begun to feed again, 5-6 ft from the joey."

Even when agonistic behaviour has developed to the stage where the joey will not approach closer than 1m to its mother away from the den, the joey when feeding, will return to within about 1m of its mother, then

move away again (e.g. Fig. 5.24 Female 6147, 268 and 272).

Presumably a joey, by returning to its mother at intervals as they feed, checks on its mother's position and is better able to maintain contact with her.

Joeys were observed to follow their mothers for most of the night during 3 all night observations (Fig. 5.25). In one (Fig. 5.25b) the joey kept within 1m of its mother all night except for two brief periods, once when left in the den, and once when it lagged behind the mother on leaving the den tree to travel on the ground. In both the other observations mother and joey separated in the early morning. One of the separations (Fig. 5.25a) occurred following an interaction between the joey and another female. In the other (Fig. 5.25c) the joey had progressively increased its distance from its mother. At first the joey had kept within 1m of the female, apart from a brief period when the female came down to the ground from the den tree. Once the female had begun to feed the joey then increased the distance between them to the order of 3-5m, and finally it was the joey who left the female. This is indicative of an increase in the confidence of the joey as the night progresses.

5.6135 Mother and Joey Separate

A third stage in the spatial relationships (following the 1m and 5m stages) of the mother and her joey is the separation of the two at night when away from the den. This was observed to occur in three contexts.

5.61351 Dependent joey is "left" by its mother

A joey who is still obviously very dependent on its mother and is still at the stage of following her closely, was occasionally seen alone.

The first and most striking observation of this behaviour occurred when Gert was seen on the ground about 200m from her den tree and without her 173 day old joey. Following agonistic interactions with another female and a male on the ground she climbed a tree. On a branch of a dead tree contiguous to the one climbed by the female was a joey sitting motionless tucked against the trunk about 6m off the ground. Although Gert did not come closer than about 5m to the joey, it was assumed to be

hers.

Another female (Jill) was observed on the ground 60m from her den tree without her 158 day old joey. When I approached she headed straight back to her den tree and climbed to the den. Her joey could be seen peering out of the den. They nose-sniffed each other then the mother began to groom about 0.3m from the den entrance while the joey remained in the den. Jill was again seen on the ground without her 139 day old joey (not the same one as above). When approached she climbed a tree but not to join her joey who was not to be seen anywhere. Two hours earlier the joey had been seen on its mother's back at their den entrance at dusk. Gert and her 154 day old joey were found 1.5m apart on separate branches of a tree. At first the joey clumsily climbed about but made no attempt to reach its mother. When the spotlight was switched off the female crossed to the other side of the tree where she fed for 1.5 hrs before returning to her joey. The joey remained in the one place, occasionally nibbling a leaf, while its mother was on the other side of the tree. Instead of returning straight to her joey Gert went to her original position 1.5m from the joey, and the joey made no attempt to join her. When, however, she did rejoin her joey they nose-sniffed, one gave a quiet grunt, and the joey climbed onto its mother's back.

Occasionally a female was seen coming out of her den at dusk without being followed by her joey. Several times Alice's joey remained in the den for short periods especially when Alice was interacting with other adults in the den tree. Alice usually returned to the den within a few minutes to join her joey.

Jill, after being trapped with her joey, entered a low den (0.5m off the ground) never seen to be used by a possum at any other time. That evening she was seen on the ground within 10m of the den, and with Jack but without her 145 day old joey. Once she returned to the den and peered into it then moved away again. After 17 min she re-entered the den to emerge 3 min later with her joey riding on her back.

I was unable to detect any definite signal given by the female and

directed at the joey when this type of separation occurred. The alternative is that on becoming separated from its mother, a joey will finally cease trying to follow its mother and remain sitting in the one place. This latter explanation is not entirely convincing because Gert's 154 day old joey was still only within 1.5m of her and could easily have joined her by moving down its branch about 2m then back out along its mother's branch about 2m. Where a joey remained in the den the security of the den may be sufficient for the joey if its mother moves away quickly, or if she is interacting with other possums. In the observation where Gert's joey (169 days old) became agitated when separated from its mother it eventually returned to their den when the male moved away, and Gert joined it 10 min later. However, 2 hrs later Gert was seen in another tree alone and her joey had probably remained in the den, because Gert returned to the den at dawn and came out a little later followed by her joey. The joey returned to the den after following Gert for only 1.5m.

Joeys who remained either close to the den or in one place when left by their mothers ranged in age from 139 to 198 days (Fig. 5.16).

I gained the impression that the female may deliberately leave her joey behind, but was unable to substantiate this.

5.61352 Travelling and feeding independently

Joeys as young as 168 days were seen separated from their mothers at night and acting independently, but still continuing to share their mother's den (Fig. 5.25 a & c).

The following observations appear to be typical of this behaviour.

Gert's joey, Gina (188 days old), followed her mother, keeping within about 1m until Gert settled down to feed in the third tree she climbed, whereupon the joey moved further away from its mother (Fig. 5.25c). For 3 hrs they kept about 3m apart, first as they fed, then for the last hour just sitting. About 01.20 in the morning the joey left the tree without any prior interaction with its mother who remained sitting. When Gert returned to her den at dawn her joey still had not rejoined her. Again,

21 nights later Gert and Gina (209 days old) were seen approaching their den tree at dawn from opposite directions, 95m apart when first seen, and probably used separate dens.

I had been watching Female 6147 and her 251 day old joey feeding in a tree 1 to 3m apart for about 5 min when at 02.31 the female descended to the ground, crossed to her den tree, and entered her den. When the female left the tree her joey continued to feed without any sign of agitation, and it was not until 1hr later that it rejoined its mother in their den. Earlier in the evening the joey had been seen following its mother from the den tree and presumably had stayed with her until the above observation.

The youngest joey observed to behave independently of its mother, was 168 days. It had kept very close to its mother, Jill, right up to the time of the separation (Fig. 5.25b). They had been feeding on the ground for about an hour, keeping about 1m apart, when at 01.36 Jill quite suddenly began to travel at a rapid walk and climbed a tree 50m away. Her joey did not follow but stood peering at Jess who had been feeding in their vicinity and with whom Jill had lost two fights earlier in the evening. This was presumably the reason for the joey not following the female. Nevertheless, when the joey did move away from Jess it made no attempt to follow its mother, but instead headed in the general direction of the den and eventually climbed a tree 35m from that climbed by its mother. Neither the joey nor its mother showed any sign of agitation at being separated. Nor did the joey rejoin Jill before she entered her den at 04.08, but presumably rejoined her there.

In none of the above observations was aggression by the female the immediate cause of the separation. Mild agonistic behaviour occurred when Jill's joey was watching Jess, but this was not between mother and joey. Nor in the case of Jill and her 168 day old joey, and Gert and her 188 day old had any agonistic behaviour been observed between mother and joey that night. However, Female 6147 had been seen to cloacal mark twice early in the evening as her joey followed her, indicating that agonistic behaviour had begun to develop in their relationship, but only of a mild

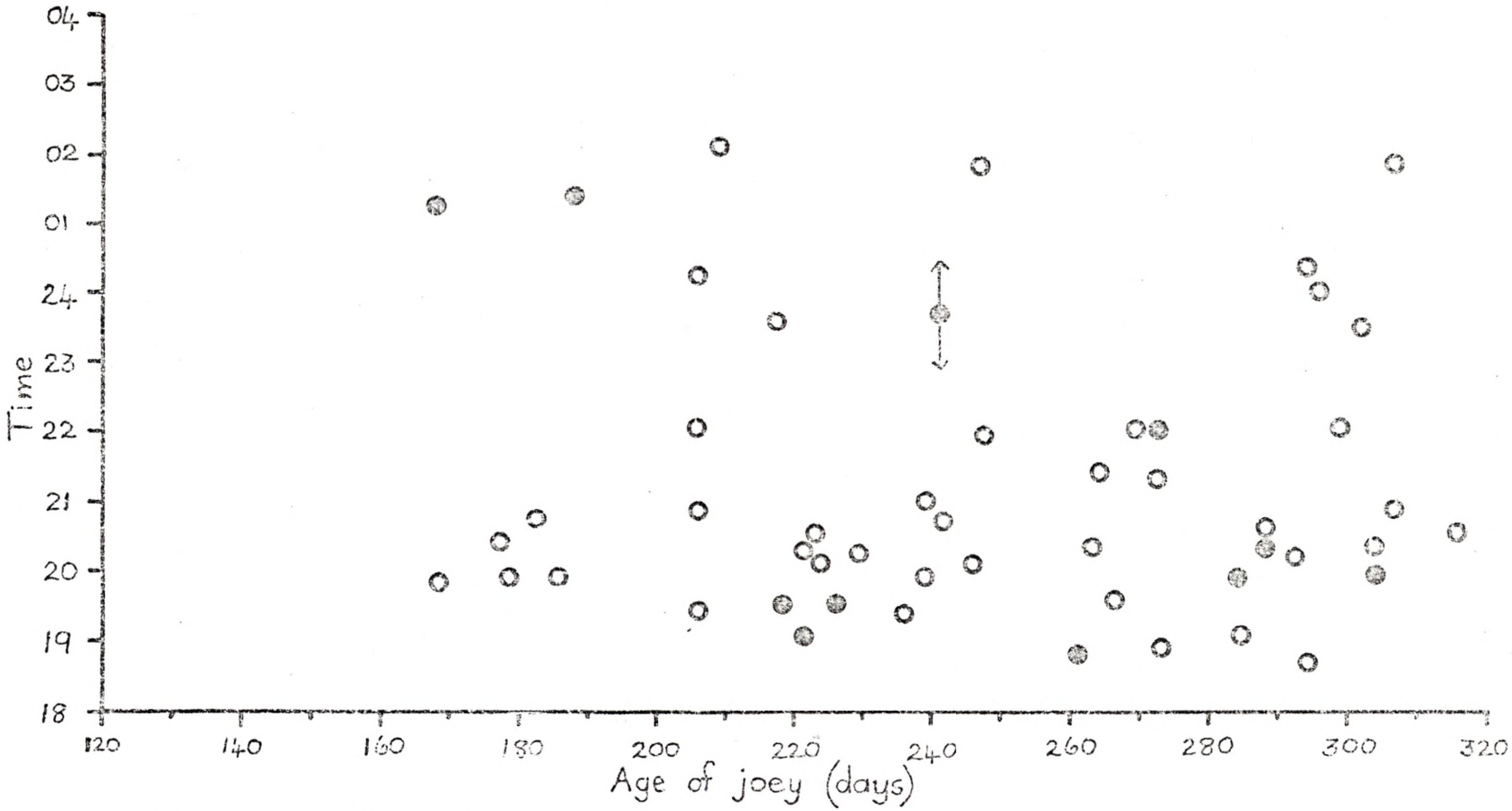


Figure 5.26 : Observations of joey separated from its mother in relation to age of joey and time of night (obs in which joey known to have been "left" excluded). Open circle = observed separated; closed circle = time at which separation occurred.

form. Also, the initiative to separate appeared to be mainly the joey's, either by leaving the tree before its mother, or by not following its mother.

Before the age of 200 days the only observations where a joey was known to travel independently of its mother while away from the den tree, were the two described above. Another group of five observations was made where the female was seen without her joey up to this age (Fig. 5.26), but in four of these only the mother was seen and in the fifth the joey had remained in the den tree. Since all five observations were made early in the night it is possible that the joey had been left in the den tree by its mother, a situation which was known to occur up to the age of 198 days (Fig. 5.16).

After 200 days, observations of mothers and joeys seen separated were common and by 210 days the time of separation was known to be as early as 19.30. The pattern of observations shown in Figure 5.26 indicates that separation occurs early in the night probably by 21.00 but in two observations it was known to occur later (between 23.00-24.30, and 22.00 respectively).

5.61353 Joey followed male

Occasionally a joey followed a male, apparently mistaking him for its mother (see Ch. 5.71).

5.614 Cohesive Behaviour

5.6141 Nose-to-nose sniffing

Nose-to-nose sniffing was predominantly a mother-joey interaction, but not common as only 12 definite cases were recorded between mother and joey.

In all 12 observations the nose-to-nose interaction preceded either the joey climbing onto its mother's back (3 obs), mother and joey coming to sit very close together (7 obs), or coming together after the joey had interacted with a male and its mother had come to its aid (2 obs). In the latter two there seemed to be an element of excitement with more intensive sniffing.

The function of the nose-to-nose sniffing was apparently to establish identity after the mother and joey had moved apart and come together again. A clear example of this was an observation of a joey hurriedly approaching its mother from the direction of two males with whom the female had had several agonistic interactions. When the joey was about 15cm away its mother raised a paw and gave a screech in an aggressive gesture. Immediately the joey stopped dead. They gazed at each other, then the joey approached slowly until coming nose-to-nose with its mother. Following a pause the joey climbed over the female's shoulders onto her back, without any further aggressive behaviour from the female. The hurried approach of the joey and the presence of the males probably contributed to the aggression directed at her joey, but following the nose-to-nose interaction this disappeared.

When Gert, who had left her 154 day old joey to feed in another part of the tree, returned to her joey, she slowed her pace when 0.3m from the joey and approached with nose outstretched. The joey remained sitting but stretched out its nose and following a nose-to-nose interaction, the joey climbed onto its mother's back. Again there had been the slowing of the approach before the nose-to-nose interaction and there had also been incipient agonistic behaviour expressed by two grunts.

A third observation of a nose-to-nose interaction was preceded by agonistic behaviour. Alice chased Alec and her 198 day old joey ran after her. The female spun round as though to lash out at her joey, but instead sniffed at the joey and allowed it to climb onto her back.

With the remaining seven observations neither a slowing of the approach or agonistic behaviour was observed in the nose-to-nose interaction. The following protocol is typical.

18.11.68 "20.00 Joey approached Gwen along the branch and came right up to her without pausing. They met nose-to-nose, Gwen leaned forward slightly as the joey approached. Gwen did not screech or attempt to stop the joey as with barely a pause it pushed under her with its head in the pouch region at 20.01."

In another 16 observations only one of the pair stretched out its

nose to sniff the other, and it was the joey in 15 of them. Usually (9/12 obs) the joey sniffed at the female's face and only occasionally (3/12 obs) at her body. A female's reaction was to ignore the joey (5/9 obs) except in three she moved her face away, and once she jerked her head towards the joey and raised a paw in incipient aggression. In the one observation of female sniffing at joey, the joey was feeding 3m above the grooming female. Suddenly the female climbed rapidly up to the joey and sniffed at it from below, sat for a moment then moved away again. The joey stopped feeding and looked down at its mother.

Although the nose-to-nose interaction was not frequently observed it is apparently one of the ways whereby possums check each other's identity. It is possibly more prevalent in situations where the level of the mother's incipient agonistic behaviour has been heightened by interactions with other possums.

The oldest joey observed in a nose-to-nose interaction with its mother was 232 days, but nose sniffing of its mother (without the reciprocal action of the female) was seen by a joey of 281 days (Table 5.36 and Fig. 5.16).

Table 5.36

Age of joey in days at which nose-to-nose and other sniffing occurred between mother and joey.

Nose-to-nose	Joey sniffed mother	Mother sniffed joey
154	178	185
170	185	
177	185	
177	195	
181	208	
185	211	
189	221	
198	236	
211	236	
213	236	
217	241	
232	251	
	251	
	281	
	281	

5.6142 "Play"

Play is not well developed in the brush-tailed possum, and in fact

some of the behaviour described as play below may be very doubtful examples. However, they do show features which fit into the very general definition of play given by Ewer (1968a, p287) ".....the essence of play is that it is not 'in earnest'".

Patting was an interaction between the joey and its mother in which either both or one of the possums gently patted at the other with its forepaws. Five such interactions were observed, and the following protocol gives an example.

31.3.67 "18.40 The joey (187 days old) came down the trunk towards Hester, who was sitting by the trunk on an horizontal branch. Joey stopped in the head down position just above Hester and began to pat at her head. Hester sitting on her haunches and patting back at the joey. It possibly started with the joey reaching out to climb onto Hester's back and with Hester responding by patting at her joey. She did not appear to be trying to prevent the joey climbing on her back as she was being very gentle. Hester then turned to face away from the joey and the joey climbed onto her back."

Typically the interactions were brief with a maximum of about four pats given by any one individual, usually only with one front paw but once with both. When both patted, contact appeared to be made with the other's paws, but when only one of the participants did the patting it was directed at the other's head. In four of the interactions the patting started following an approach by either the joey or the female (Table 5.37).

"Play" biting was observed twice in which the joey gently bit at its mother's face, and in one of the observations the mother may have responded in a similar fashion. Play biting occurred once in conjunction with patting as in the following protocol.

11.10.68 "18.40 Joey (195 days old) got off Jill's back and sat immediately below her. Joey appears to be licking Jill's face and the female is lifting her chin up out of the way. Jill has now turned to groom and joey just in front. 18.41 Joey sitting in front and is reaching up to Jill's chin apparently trying to bite at her chin, and at the same time patting at Jill's face with its right paw. Jill did nothing apart from lift her head, then bounded up the tree with the joey following."

In the second observation Jill and her 336 day old joey were sitting side by side touching. Their heads were moving about and from a distance it appeared as though they were "play" biting at each other's faces.

Both patting and play biting may be incipient aggression, and in

Table 5.37

Summary of "play" behaviour

Type of play	Age of joey (days)	Active Participants	Behaviour Before	Behaviour After
Patting	159	Mother & joey	Female approaches	Joey onto back
Patting	187	" " "	Joey approaches	" " "
Patting & biting	195	Joey only	Sitting touching	Joey followed
Patting & scuffle	267	Mother & joey	Female approaches	Sitting touching
Patting & biting	7-8 mths	" " "	Sitting touching	" "
Biting	336	Female only	Joey approaches	Joey withdrew

Table 5.38

Allogrooming between mother and joey

Groomer	Age of joey (days))	Length of grooming bout (mm)	Area groomed	Type of grooming
Female	143	less than 2	?	mouth
Joey	158	" " 1	back & shoulders	licking & biting fur
Female	170	" " 1	back	mouth
"	174	" " 1	"	"
"	177	" " 1	?	"
"	185	" " 1	back	"
"	188	Spasmodic for 30	shoulders	"
Joey	191	less than 2	back of head	"
"	195	" " 1	face	licking
"	195	" " 1	back of head	vigorous mouth
"	215	" " 1	flank	nuzzling
"	6-7 months	?	tail	biting & pulling fur
Female	7-8 "	4 to 12	top of head	licking & biting fur
Joey	230	less than 2	back	mouth
"	281	" " 2	neck	licking

two observations the interactions progressed beyond the gentle patting. When Jill rapidly approached her joey, the joey gently hit out at its mother. There was a mild scuffle and a faint screech in a very mild agonistic interaction. Following it the mother and joey sat touching. In another observation the joey approached its mother to sniff at her. The female was half out of the den and as the joey approached on a horizontal beam below her, she batted at the joey, who reacted by withdrawing less than 0.3m. Several times the joey approached and gradually the female's gentle pats became blows accompanied by attempted bites and a screech, behaviour which was now obviously aggression directed at her joey.

However, the play component of patting and play biting is indicated by the predominance of contact behaviour immediately following the interaction (Table 5.37) and only in the last described interaction in which the aggression was obvious did the interaction result in the participants drawing apart.

"Play" was so rarely seen (6 obs) that it can be considered to have only a rudimentary role in the development of agonistic behaviour.

5.6143 Allogrooming

The only allogrooming observed was between mother and joey up to the age of 281 days (Table 5.38), and at no time was reciprocal allogrooming observed. The number of grooming bouts observed was low (15), but it is possible that most allogrooming took place within the den. Duration of each bout was brief, usually less than one minute (Table 5.38), except in one observation when more or less continuous grooming lasted at least four minutes, and in another a bout of spasmodic grooming continued for 30 min while a mother and joey sat touching.

Joeys groomed their mothers equally as often as mothers groomed their joeys, but the type of grooming tended to vary according to who was the groomer. When a female groomed her joey she invariably groomed the joey's back, or the back of its head as it sat in front of her. Usually she mouth-groomed her joey in a desultory non-functional manner for only a brief period.

However in the 4 min observation the female was licking and biting the fur on the back of her joey's head, in much the same manner that a domestic cat does to her kittens.

Joey's grooming of its mother, on the other hand, was more variable. It did not confine itself to grooming its mother's back or shoulders; it at times groomed the side of its mother's face, neck, flank and even once groomed its mother's tail by holding the tail with its front paws as it bit and pulled at the fur with its teeth. Also the type of grooming was more variable as licking and nuzzling were features not performed by the female. The nuzzling may have had connotations of suckling but it was well away from the opening of the pouch. Twice a joey (191 and 195 days) mouth-groomed the back of its mother's head while it was riding on her back (Table 5.38).

Response by the animal to the grooming was minimal without any evidence that it solicited the grooming. When a joey licked at its mother's face the female lifted her head away apparently to avoid the licking. In one bout of vigorous mouth-grooming of the back of the mother's head the female lowered her head during the bout, thus making it easier for her joey to reach the area being groomed.

There was no evidence that allogrooming had any cohesive social function. Even the purely functional aspect of fur cleaning was minimal by the time the joey had ceased to use the pouch away from the den. While in the pouch, and possibly when first out of the pouch in the den, a female may clean her joey's fur by mouth-grooming it.

5.6144 "Suckling"

A joey will crouch on the branch in front of its mother with its head under the female in the pouch region. Usually the female sits quite still in an upright, rather hunched position caused by the joey being wedged under her, with her front legs down each side of the joey's flanks and her chin just above the joey's back. Once she was seen with her chin actually resting on its back and once or twice she groomed the joey's back. Side to side movements of the head by the joey were sometimes made,

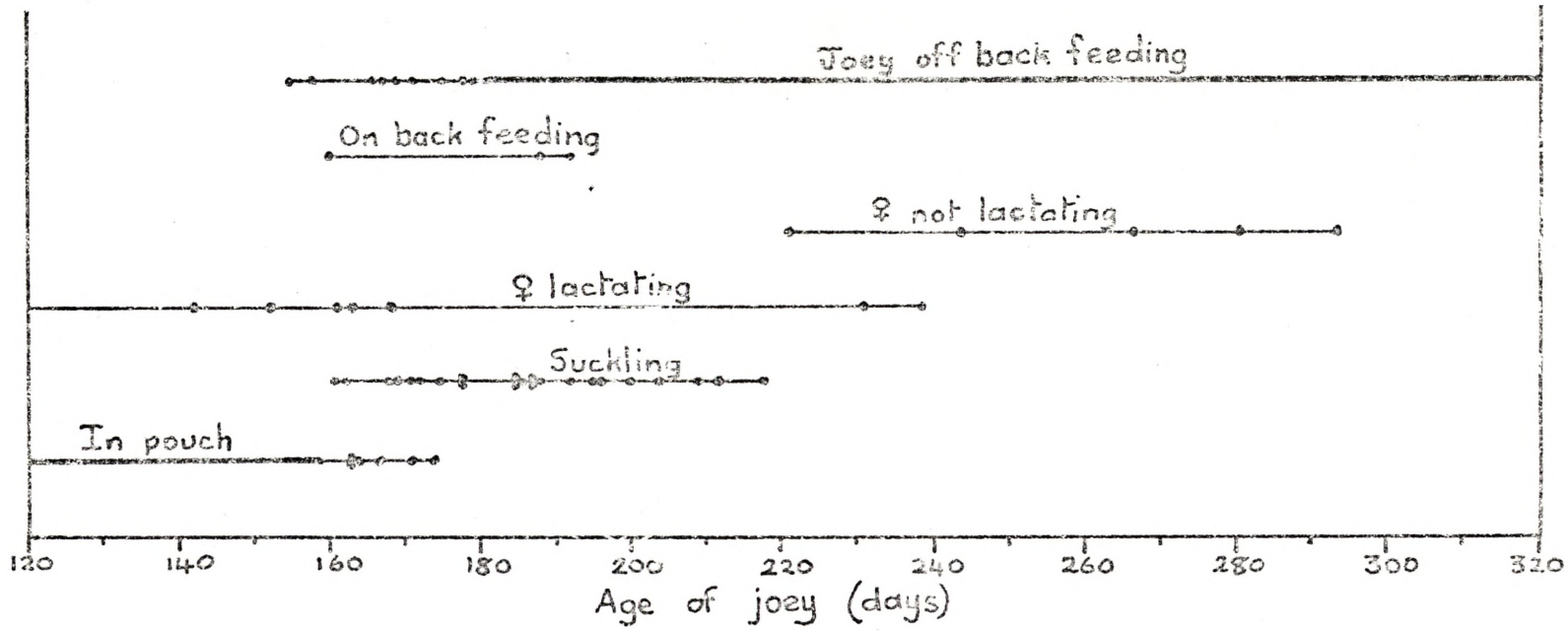


Figure 5.27 : Suckling and eating by joey in relation to age and lactating condition of mother. Dots = actual observation; thick line = numerous obs; thin line = range of obs.

apparently reaching to open the pouch, but nudging movements were not observed. Sometimes a female sat with her front paws resting on a higher branch, or with her hind legs straddled across two branches, thus exposing the pouch region, and once a joey was seen sitting on a branch below its mother with its head pushed into the pouch region. In one observation the joey was pushing hard under its mother in an apparently unsuccessful attempt to make her sit upright so that it could reach the pouch opening.

There seems little doubt that a joey in the above position was usually suckling, although only once was it actually seen with its nose buried in the pouch. This is supported by observations of female lactation which continued beyond the age of the eldest joey seen in a suckling position, and that the first non-lactating female with a joey was not recorded until after the last observation of suckling (Fig. 5.27).

However, some observations of "suckling" may have been attempts to enter the pouch rather than to suckle, and even past the age when a joey had ceased to enter the pouch, pushing its nose into the pouch may give the joey a sense of security. This was most clearly shown by two observations of joeys aged 194 and 199 days. In both observations the joeys were sitting within 0.3m of their mothers and when I shone the spotlight on them the joeys immediately pushed into the suckling position.

The length of time that a joey maintained the suckling position ranged from 0.25 to 35 min with a mean of 7.98±2.65 min (Table 5.39). In the two longest observations of 35 and 25 min both female and joey were almost certainly resting.

Table 5.39

Length of time joeys spent in the suckling position. Figures in brackets not used in statistics.

Time (mins)
0.25
0.5
1
1
1
2
3
(3-4)

Table 5.39 cont.

Time (mins)
6
(5-10)
10
10
12
25
35
Mean 7.08
S.D. 9.9258
S.E. 2.6527

5.6145 Touching

A joey may sit next to its mother actually touching her. There was no fixed orientation of the two possums evident when sitting touching, and the joey could be either in front of or behind its mother.

Touching was not just a stage in a joey climbing onto its mother's back because there was a definite trend for it to continue after a joey had ceased to ride on its mother's back. (Table 5.40).

Table 5.40

The age in days of a joey when last seen riding on its mother's back and when last seen touching her.

No. of Obs	Age of last obs of joey riding	touching	No. of days touching exceeded riding
11	167	336	+169
	154	129	+129
	153	251	+ 98
	198	226	+ 28
	199	225	+ 26
	198	222	+ 24
	195	208	+ 13
	173	185	+ 12
	206	217	+ 11
	187	194	+ 7
	298	304	+ 6
4	181	181	0
	182	182	0
	188	188	0
	229	229	0
2	210	192	-18
	198	171	-27

After 242 days all observations of touching occurred in a den tree (Fig. 5.16) usually soon after mother and joey emerged from the den at

dusk to sit just outside the entrance.

Touching is one of the behaviours of the contact phase in the social relationship of a mother and her joey and will be discussed later (Ch. 5.6145).

5.6146 Mother's reaction to joey in distress

A female will wait for her joey if it becomes separated from her in a tree, but will not immediately return to its joey to retrieve it.

One context, however, did elicit a strong reaction by the female to her joey in distress, and occurred when a joey had an interaction with a male (8 obs). Typically this occurred when a mother and joey were in a tree more than 3m apart as this enabled the male and joey to meet without interference from the female. Irrespective of whether it was a male or joey who approached, when about 0.5m apart the joey gave a subdued screech. Immediately the joey screeched, its mother moved hurriedly towards it, from distances up to 6-7m away. Usually the rapid approach of the female made the male give way quickly and only once did the female chase the male. She chased him down the tree to the ground, then returned to her joey and they met nose-to-nose.

In one observation the approach of a male giving shook-shook calls brought Jill rapidly down to join her joey before any interaction took place between the male and joey. In another Jill and her 177 day old joey became separated, and despite the presence of a male in the tree above the joey Jill seemed unconcerned. When however her joey approached within 2m of the male Jill hurriedly returned to her joey. Despite her apparent unconcern, Jill may have been well aware of her joey's movements in relation to the male, because no screech was heard to attract her.

One interaction took place on the ground. Male 20 bowled Hester's 187 day old joey over and pinned it to the ground. Immediately both Hester and Donald rushed back to the joey and Donald chased the attacking male.

Twice a joey interacted with another female. In the first, Eve climbed a tree already occupied by Iena and chased her 209 day old joey, giving a quiet growl/chatter. When the joey was cornered at the end of

a branch Eve turned and chased the joey's mother who had made no attempt to intervene but merely sat and watched. In the second observation Jill's young joey of 163 days became cut off from its mother by Jess after a fight won by Jess. Several times the joey came down towards Jess in an attempt to reach its mother but each time turned back when level with her, without any vocalisation. Meanwhile its mother remained near the base of the tree 3m below them but made no attempt to retrieve her joey.

The lack of interference by the mother in the interaction between its joey and the other female was probably because of the other's subordinate status in each case.

When a joey's distress was caused by myself the females reaction was different, though variable, presumably because of my presence.

Without any difficulty I caught Alice's 177 day old joey as it attempted to bound through tall stiff weed stalks on the ground. Alice went up a nearby tree and merely sat and watched me during the 5-10 min that I handled the joey, who made no vocalisations even when ear clipped. Even when the joey climbed up her tree after release Alice made no attempt to rejoin it. Alice was an exceedingly shy animal and my presence undoubtedly inhibited her behaviour.

Under similar circumstances when I caught Female White-tip's 175 day old joey on a tree base, the mother came down her tree onto the ground 6m away, but did not approach any closer. Her joey had given two very quiet calls as I approached it and 2-3 screeches as I handled it.

In complete contrast was Female Worm-ear's behaviour when I handled her joey who was still riding on her back and pushing its head into the pouch, therefore less than 220 days old. The female was sitting on a low branch and allowed me to approach and gently ease her joey from under her. As soon as I did this the joey gave a shuck-shuck call and the female reached out towards my arm. I let the joey clamber onto her back but a moment or two later prized it off again and stepped back a metre. It gave a shuck-shuck call; the female gave an answering shuck-shuck and began to come down the tree trunk apparently looking for her joey. When I held out

my arm with the joey on it, the female grasped my arm, and the joey climbed back onto its mother. One of them then started to give buccal clicks.

It is apparent from these three observations that the mother's behaviour was probably dependent on the degree of caution with which she reacted towards me, ranging from complete inaction in the case of Alice to apparent complete lack of fear in the case of Moon-ear.

Finally one mother showed a very strong reaction to the distress call of a young magpie lark (Grallina cyanoleuca) which I captured at night. The bird gave loud distress calls and a female possum came bounding towards me, climbed over a 2m wire mesh fence and down onto the ground no more than .75m from me. She was very agitated and ran about on the ground both towards and away from me 3 or 4 times before climbing back over the fence and up a tree 15m away to join a young joey sitting quietly in a low crotch. The joey immediately climbed onto its mother's back. Apparently the mother had left her joey in the tree while she fed on the ground. It is possible that she had mistaken the young bird's calls as distress calls of her joey, though to my ears there was no great similarity.

5.615 Agonistic behaviour

Agonistic behaviour between mother and joey begins to develop when the joey is still travelling on its mother's back.

Apart from a mother moving forward to encourage her joey to slide off her back, or to discourage it from climbing onto her back, the female exhibited aggression of varying intensity directed at her joey.

5.6151 Female aggressive behaviour

5.61511 Shrug (1 obs)

The mildest form of aggression observed was an "impatient" shrug of a shoulder by the female when her joey placed a fore paw on it, and the joey dropped its paw back to the branch.

5.61512 Head turn and raised paw

When a joey approached from behind to climb onto its mother's back the female jerked her head round and partly twisted the front part of her

body round as she raised a front paw (6 obs), or only the paw was raised if the joey approached from in front (2 obs). In all but two of the observations the head turning and paw raising were little more than intention movements to either bite or strike. They were potential threat behaviours though the joey apparently did not recognise them as such. For instance in one observation female White-tip turned and raised her paw as her 187 day old joey scrambled over her rump, without a pause, onto her back. Female White-tip did not strike at her joey but almost immediately turned forward again and began to feed. At other times the female's threatening gestures appeared to be directed unintentionally at her joey. When Alice, for example, chased Alec and her joey ran after her, she spun round to threaten her joey with a raised paw. Almost immediately, however, her aggression subsided, presumably on recognising that it was her joey and not another possum, a mistake possibly made at the height of the chase. They met nose-to-nose and the joey climbed onto her back. A mere rapid jerk towards her joey as it came to sit beside its mother was the mildest expression of this form of aggression and sitting up on her haunches with both front paws raised ready to strike accompanied by several short quiet screeches was the most intense expression.

In one observation Ella's 181 day old joey approached its mother and attempted to mount from behind, but was prevented from doing so by the female half turning and biting and hitting out at her joey. After what appeared to be a brief scuffle, the joey shot back up the branch about 1m. Three to four times the joey approached its mother and each time retired after a brief scuffle. The scuffles were relatively mild and at the time I thought the joey may have been playing. However, the fact that it was obviously attempting to climb onto its mother's back and was not succeeding argues against play. Only 3 min earlier the joey had been seen on its mother's back, but it was not observed whether the female forced the joey off her back. In a second observation of the same female but with a different joey about 7 months old, the mother exhibited persistent and varied aggression towards her joey. The observation is given in the

following protocol.

5.11.68 "19.24 Ella moved away from joey who kept very close behind her, and it may have tried to climb onto her back. The female turned half round impatiently two or three times. There was a mild screech and the joey began to come down the branch followed by the female. Female chased joey about 12ft down the branch. The joey would stop, briefly, the female catch up, and joey run ahead again. It was a definite chase, but a mild one. Female then moved back up the branch away from the joey to about 8ft above the joey.....19.36 joey has come back down the branch and is level with the female, both looking at each other. Joey.... has gone right up to the female, they met nose-to-nose. Female coming down (only 2ins) and joey gave way, not a chase. Female lunged at joey who came down the branch followed by mother. Female made another lunge at the joey - this is about 2 to 3 lunges she has made, only mild ones. Female stopped and moved out along another branch, joey 3ft below her.....19.41 joey again approached mother, there was a mild screech. Did not see what happened but when I looked female was chasing joey down the branch. Joey rapidly moving through foliage, female following. Joey went out to the end of a branch and turned (cornered) to face female, who stopped 6ins from joey then turned and retired to 2ft from joey. Now going on down branch from joey."

Two other forms of female antagonistic behaviour - supplanting and chasing - also occurred in the above interaction.

Once a female was seen to walk up to her 298 day old joey from behind and gently bite it on the rump, causing the joey to move away 10-12cm.

5.61513 Supplanting

Several times a female was observed to approach or follow a juvenile steadily and persistently. The most obvious expression of this as an aggressive behaviour occurred when a female approached a cornered joey following an agonistic interaction (4 obs). In the above protocol the female turned back when about 15cm from her joey. However, in two other observations the outcome of the interaction was that the joey fell from the branch. In one of these, three possums bounded up a tree with a juvenile going out to the end of a low branch. A female walked steadily along the branch towards the juvenile who was crouched watching her. When about 1m away the juvenile backed and gave a screech. As the female continued to approach, the juvenile made 2-3 short leaps towards the female, as though trying to jump past her. On the last leap it caught a thin branch below the female, but fell to the ground when the branch broke. In a second observation I heard a thud and saw a female at the end of a

branch 3m off the ground looking down at a juvenile who had obviously just fallen to the ground. The juvenile had probably been supplanted by the female in an interaction similar to that described above, as there had been no noise of a chase. The female then came down to the ground and chased the juvenile briefly. In neither observation was it known whether the female was the mother.

Female 6147 and her 272 day old joey had been feeding 1-2m apart. When she approached her joey it hurriedly gave way. It went out to the end of the branch then turned and crouched, staring at the female who was following at a slow but steady pace. Female 6147 stopped 0.5m from her joey, there was a mild screech, probably made by the joey, and the female turned and moved away.

The four examples given are cases of the female supplanting a juvenile. There was no evidence of an actual attack, although in two it resulted in the juvenile falling to the ground. In the other two the female turned back before the joey was forced to take evading action which had resulted in falls for the other two.

Another rather different case of supplanting behaviour took place between Alice and her 273 day old joey. It was early in the morning and Alice had returned to the base of her den tree, but instead of climbing it she continued to a small tree 20m away in which her joey was feeding. She sniffed carefully at the base and at the trunk of the tree as she climbed it. Alice stopped 2m below her joey, did not look up at it, and began to feed. By this time her joey had stopped feeding and was peering intently down at her. Soon afterwards the joey began to descend, making a dash past its mother who was sitting beside the 10cm diameter trunk. I could not see how Alice reacted except that she remained seated. Her joey left the tree and climbed into their den tree. Alice's actions throughout gave a distinct impression of supplanting her joey from the tree despite the fact that she did not actually approach any closer than 2m.

In general when a female chased her joey it was a relatively mild interaction concerned mainly with preventing or discouraging the joey from coming too close to her, for example the chases already mentioned.

Another example of mild chases occurred when a tame female was being fed by hand. Her joey kept approaching in an attempt to also take the food, but each time that the joey came within about 15cm the female chased it for about 0.6m.

The most aggressive chase observed of this type, i.e. the maintenance of social distance, took place between Gert and her 255 day old joey. Gert and her joey had come out of the same den. Twenty minutes later the joey came down the den tree closely followed by Gert in a give-way cum mild chase interaction. There were several pauses and at times the female came right up with the joey but did not bite or strike at it. Just before reaching the ground the female passed her joey and jumped to the ground indicating that the joey was giving way rather than the female chasing. About half an hour later they were both again on the ground with Gus nearby. Suddenly Gert made a dash at her joey who was 3-4m away, and the joey spun away from her to spring onto the base of a nearby tree. As the joey clung to the tree Gert made a second dash at the joey and the joey jumped to the ground. Following a brief pause Gert chased the joey. The joey bounded up a tree closely followed by Gert, but when only 1m up the joey became flustered, missed its footing, and fell to the ground. It stopped 1m from the tree crouched on the ground looking up at Gert who was 1m up the tree in the head down position. Suddenly Gert leapt at her joey, but the joey managed to dash to one side. Gert was after it in a flash and caught hold of the joey's rump, but the joey managed to scramble free and bounded to one side, stopping 3-4m away. It appeared to be running away from Gert, but at the same time keeping fairly close to her thus exhibiting ambivalent behaviour. Soon afterwards however, the joey moved 15m from Gert, who first watched her joey move away then followed slowly. Soon after this they drifted apart and began to travel independently.

In another observation the joey appeared to become flustered when chased by its mother. Female 6147's 298 day old joey made an alarm leap onto a tree and peered down at the ground, presumably at its mother who was hidden from my view. The joey then jumped to the ground and immediately the female chased it for about 2m. Both stopped and stood immobile for a moment before the chase was renewed. The joey then leapt into the air waving its legs about as though trying to catch hold of a tree trunk that was not there. Female 6147 did not actually attack her joey even when the joey made the flustered leap into the air, but instead she turned aside.

Three chases were typical of the type in which one possum displaced another from a tree. For example, Emily and her 218 day old joey had been feeding about 7m apart when the female crossed the tree and approached her joey. When 2-3m away the joey began to scramble rapidly down the tree and a chase started. At one stage the female increased her speed and came level with her joey's tail, but the joey in turn also increased its speed. The joey stopped 1 to 1.5m off the ground with the female 1.5m above it, but when the joey jumped to the ground the female remained clinging to the trunk for 6 min before also jumping to the ground.

Twice a mother was observed to chase her joey out of her den. In one the joey had returned to the den at dawn before its mother and was displaced when the mother returned. It was barely a chase and the joey almost certainly entered the den again soon afterwards. The second observation was much more aggressive. At 01.14 subdued screeches and a series of grunts attracted me to a large dead den tree. Female Moon-ear was high on the trunk looking down at her 255 day old juvenile below her. There had obviously been a chase and the female was screeching quietly as she gazed at the younger possum. Another chase developed with screeches and grunts and lasted for 6m with the two possums stopping 3m apart looking at each other. I approached and the female entered a den followed shortly afterwards by her joey. There were no vocalisations. However, 4 min later the joey shot out of the den with its mother chasing, her nose level with the joey's tail. She gave a brief gutteral chatter.

The female returned to the den entrance after only a 2m chase.

5.61515 Fight (5 obs)

Fights were rare and relatively mild between mother and joey. Two have already been described following other agonistic behaviour. In one Ella bit and struck at her 181 day old joey, thus preventing it from climbing onto her back. In the other Gert briefly caught hold of her joey's rump following a chase on the ground.

A third brief scuffle occurred when Female 6147, following 2 to 3 mild agonistic interactions, approached her 272 day old joey along a branch just above the joey. The joey looked up at its mother but did not give way, and the female jumped down on top of her joey. There was a very brief mild scuffle, with a subdued hiss, and the joey moved down the branch.

In the fourth observation Female 6147 walked towards her 298 day old joey, who was hanging head down on the main trunk, and gently bit the joey on its rump. Immediately the joey moved rapidly round the trunk a few centimentres, then moved about 1m below the female.

Only once was a relatively aggressive fight seen. The Tyne St. female had chased her 9-10 month old juvenile out of the roof one afternoon well before dusk, and when the juvenile tried to return, the female came out of the entrance and caught the juvenile by the root of the tail and held onto it for 4-5 sec as the juvenile attempted to pull away. The female gave two growls while she had hold of the tail. The joey never made any attempt to retaliate in the above agonistic interactions.

5.61516 Stare

Twice a female was observed to stare at her approaching joey in an aggressive manner. Once a brief direct stare coincided with the joey stopping 1m from its mother, then turning and moving away. In the other observation the joey gradually moved towards its mother as it fed. The female was gazing intently at her approaching joey, and when it suddenly stopped feeding and looked towards her from 1m she rushed at the joey and a chase followed.

Observations of the female watching her joey were relatively common,

but they lacked the intensity of the stare. For example a 298 day old joey was approaching its mother from behind, but suddenly came to a halt 0.75m from its mother who had her back to the joey but her head turned looking at it. It appeared that the joey had suddenly noticed its mother looking at it and so stopped.

5.61517 Olfactory

As already discussed in Ch. 4.23112 a high proportion of female chinning and chasting, and all observations of cloacal and urine marking occurred when the female had a joey following her.

Evidence that olfactory marking is an indirect agonistic behaviour rather than an attractant to her joey as suggested by Bolliger and Hardy (1944) is based mainly on a series of observations made on Female 6147. No olfactory marking was observed during the first three 90min observation periods when her joey was 191, 236 and 241 days old respectively. Thereafter olfactory marking by her was seen on five out of the nine nights she was under observation (Fig. 5.24 Female 6147, 251, 253, 268, 275 and 298). This coincided with a pronounced change in the distance between mother and joey after they had left the den tree, certainly from day 253 on as shown in Figure 5.24. It could be argued that because of the increased distance there was more need of a cohesive type marking as suggested by Bolliger and Hardy (1944). However, observations show that the female olfactory marking was associated with agonistic rather then cohesive behaviour as indicated in the following examples. Female 6147 chinned and chasted a branch then urinated on it as she came down a tree closely followed by her 268 day old joey. However, her joey appeared reluctant to come within 1m of its mother and watched her intently as though ready to withdraw rapidly. When 275 days old the joey allowed its mother to move into the tree adjacent to the den tree before following. When it did follow it stopped 1.5m above its mother, then approached her slowly, staring intently at the female who had her back turned. Joey stopped 0.3m from female but appeared very nervous because when the female moved slightly the joey drew back suddenly. The female continued on down

taking no apparent notice of her joey, but she did chin and possibly chest a branch then lowered her hind quarters to waddle along the branch a couple of paces as she urinated along the branch. The joey followed but came no closer than 1m and throughout the descent stared intently at its mother. It took no apparent notice of the branch marked by the female. Once on the ground Female 6147 still continued to apparently ignore her joey but she did chest the base of a tree she passed, and the joey continued to watch its mother intently, and paid no attention to the marked tree. During the rest of the 90min observation period the joey gave-way to its mother at least twice, there was one mild chase when Female 6147 suddenly rushed at her joey who was sitting 1m away, and the female at least once stared intently at her joey. All this time the joey had been watching its mother intently and not coming closer than about 1m, but at the same time following her. Apart from the first 13 min spent sitting together at the den entrance for the rest of the observation the joey had shown clear ambivalent behaviour in that it followed its mother apparently torn between coming close to her and an apparent fear of its mother, expressed as intent watching of her, and rapid withdrawal when its mother made a move towards it. Similar behaviour was exhibited by the joey at the age of 298 days when olfactory marking by its mother and several definite agonistic encounters took place.

Because olfactory marking is associated with agonistic behaviour such as a chase, stare, and more especially with a joey's reluctance to approach its mother closely, it is considered to be aggressive behaviour. A joey was not observed to respond to a scent mark deposited by its mother, but a young possum may nevertheless come to associate such marking with aggressive behaviour. This raises the question of whether a possum instinctively recognises a scent mark as an aggressive signal, or whether the scent mark merely conveys information relating to the presence of the marker and that the possum sniffing the scent reacts according to previous experience relating to scent of that kind.

5.61518 Auditory

Most agonistic interactions between mother and joey were silent. In 32 interactions involving give-ways, chases and fights, only seven were accompanied by mild screeches, one also with a grunt (Table 5.41). In the give way encounters both the screeches were given by the joey as it crouched watching its mother approach, whereas with the chase it was the female screeching in two, with the other two uncertain. A gutteral brief chatter was given by a female as she chased her 255 day old joey out of a den, and in one chase a fast shook-shook was given by one of the participants.

Table 5.41

The number of mother-joey agonistic interactions accompanied by vocalisations.

	Type of interaction						
	Give-way		Chase		Fight		
	with	without	with	without	with	without	
Screech	2	13	4	9	1	1	30
Grunt			1+				1+
Brief Chatter			1				1
Shook-shook			1				1
Total	2	13	6+	9	1	1	32+

+ Accompanied screech, thus lumped for purposes of total encounters.

This lack of vocalisation is interpreted as indicative of the mild nature of most agonistic interactions between mother and joey, not as in the male-male interactions where the relative silence of the interactions is interpreted as indicative of the obviously more intense nature of the interactions.

One series of subdued screeches and grunts (not included in Table 5.41) given by a female appeared to indicate ambivalent behaviour directed at her joey. I heard a subdued screech come from the direction of Female 6147 and her 288 day old joey, who was about 10cm from its mother. The female then gave a sudden grunt, turned round and began to come down the tree. As she descended she gave several grunting screeches of high intensity but without turning to look at her juvenile who was following 0.6m behind. Following the vocalisations she kept her mouth open until she stopped in a crotch 1.3m below the den, turned to look up at the juvenile

and continued to grunt and screech. The juvenile had not stopped or paused when the female vocalised as she descended, but it did stop about 0.5m above its mother when the latter turned to look towards it. The female turned to look at me then back at her juvenile with her mouth open before giving another grunt and screech. When she turned away again her juvenile began to approach very slowly. They then both continued down the tree without any further vocalisation and with the juvenile following within 1m.

The meaning of the behaviour described above is not clear but it is taken to be a display of incipient aggression by the female by means of vocalisation, but unaccompanied by a confrontation with her joey except briefly at the end.

5.6152 Joey agonistic behaviour

5.61521 Give-way (12 obs)

When Ella bit and struck at her 181 day old joey as it attempted to climb onto her back, the joey was forced to move away from its mother. However, it was not until a joey was older (226 days) that true give-way behaviour was observed; with a joey giving-way to its mother without the necessity of direct aggressive contact.

A joey gave-way to its mother in a number of contexts. When below its mother in a tree, and she began to descend, it either waited for her or descended ahead of her. When it did move ahead of her it was apparently giving way to her in an agonistic interaction rather than merely moving in front of her. If the female caught up with the joey the joey increased its speed to draw ahead so that they were separated by about 0.5m. In one of the examples of the direct stare the joey turned and moved away from its mother in a give-way interaction. In a similar interaction a joey had cautiously approached its mother and stopped 2m away gazing intently at the female. The female merely turned her head and looked towards the joey, and it immediately turned and retreated. A female who had been feeding 1.5m from its joey, stopped and moved towards the joey (not aggressively). When 0.6m away the joey turned and hurriedly climbed

higher.

A feature of the give-way behaviour was that the mother and joey were usually between 0.3 and 1m apart when the joey actually began to retreat in a give-way interaction (Fig. 5.28).

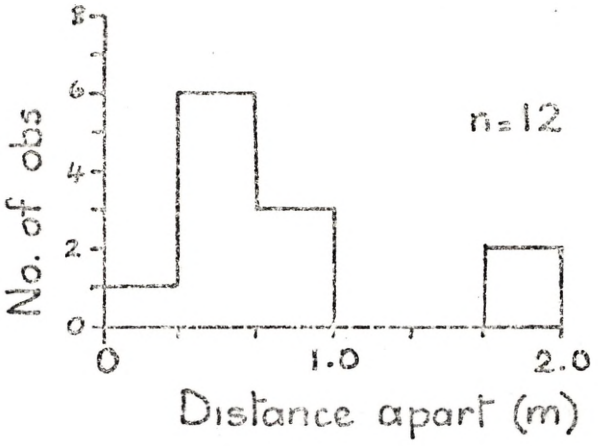


Figure 5.28: Distance between mother and joey when joey began to give-way.

5.61522 Cautious approach

Together with the give-way the joey may show a marked change in its bearing when approaching its mother. Instead of coming right up to her without any sign of submissive behaviour, the joey may approach slowly and cautiously with the appearance of being ready to move away. The clearest case of the cautious approach is given in the following protocol.

21.1.69 "19.46 Joey on the branch 6 ft from female (6147) looking down at her with ears cocked forward and head thrust forward. Female, sitting transversally on branch, turned her head to look up at joey. Joey immediately turned and went back up the branch (give-way), so now 10 ft above her. Joey turned and came down the branch 18 ins towards female looking down at her with its ears cocked forward. Female sitting diagonally on branch looking into the night. Joey coming on down staring at the female, ears forward and body low and held back in relation to the legs - indicating readiness for flight. Female has not looked up at joey 6 ft above her. Joey standing motionless staring down at the female. 19.50 Female turned and is moving down the branch away from the joey, without looking up at the joey. The joey watched female for a moment then turned and moved up the branch away from female."

Ears cocked forward and gazing intently at its mother are the main features of the joey's cautious approach. In another observation the joey came slowly down towards its mother staring intently at the female who was sitting with her back towards the joey. It stopped about 0.3m

above its mother but appeared very nervous, because when the female moved slightly it moved back quickly. The longest observation of this type of behaviour lasted for nearly half an hour. The female had been slowly descending a tree with frequent stops followed 1-2m by her joey which kept watching its mother intently. For the last 15 min the female sat on the lowest branch with the joey 0.6m from her. For about the first 5 min the joey sat staring intently at the female then looked away. For the next 10 min it sat staring into the night but frequently looking at the female.

As with the give-way interactions which were closely associated with the cautious approach or follow, a joey never came closer than 0.3m of its mother following such an approach. There seems little doubt that the cautious approach with the joey intently watching its mother is an agonistic reaction to possible aggressive behaviour by the female.

5.61523 Ambivalent behaviour

When a joey approached its mother cautiously it showed ambivalent behaviour in that it was approaching its mother but at the same time prepared for rapid withdrawal.

Three other cases of ambivalent behaviour were observed. In one of these Gert's 289 day old joey spent 26 min moving backwards and forwards along a number of small branches in a fig tree, but always keeping from about 1.5m to 2m from her. He was not feeding but continually began to approach Gert only to turn round and move away again. This approach and withdrawal kept up more or less continuously for 26 min. Eventually he ran towards Gert and passed underneath "sloth-like" on the same branch, and stopped 2m further along the branch. There was a subdued screech and a grunt as he passed and Gert lashed out at him with a fore paw without shifting from her position. Alternative routes round his mother were available, and it was concluded that the joey's behaviour showed ambivalence between wanting to approach his mother, yet being afraid to do so because of maternal aggression displayed when he finally completed an approach. In another observation Eve's 229 day old joey bounded after

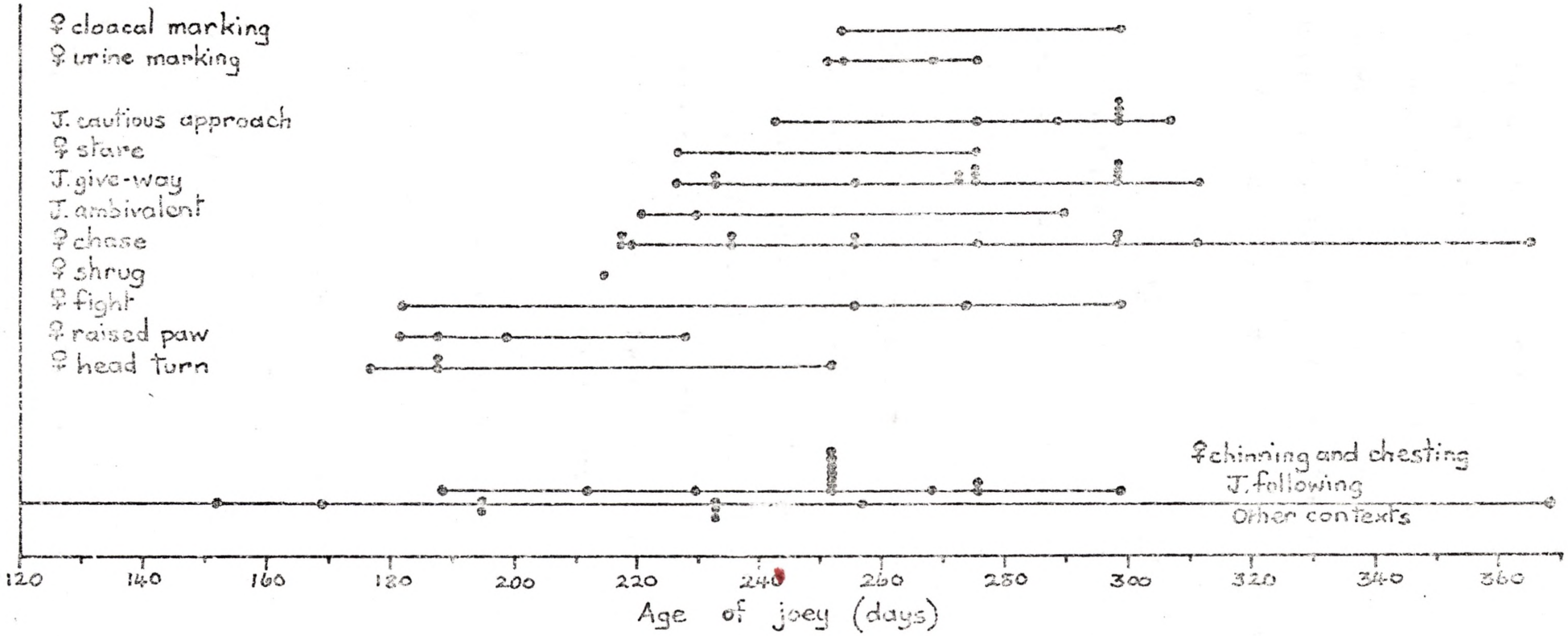


Figure 5.29 : Mother-joey agonistic behaviour, in relation to age of joey, observed during the 90 min observation period from time of emergence from den (all obs of olfactory marking by female included). Dots = obs; horizontal line = range.

its mother on the ground. On reaching her it appeared to spring vertically into the air, as though it had intended to jump onto its mother's back but had changed its mind at the last moment. The third observation was similar in that Alice's joey (220 days) came dashing out of the den and jumped onto its mother's back. It landed awkwardly, half on and half off, then tumbled over Alice and almost fell off the branch. The impression gained was that the joey had attempted to hurriedly dismount virtually before it landed.

5.616 Development of Agonistic behaviour

On examining the onset of the types of agonistic behaviour in relation to age of the joey (Fig. 5.29), it is apparent that some types develop well before others.

Observations of female chinning and chesting were concentrated in the period from the time a joey had started to get off its mother's back to the final independence of the joey (Ch. 4.23112). However, some observations were made when the joey was still in the pouch. It has been argued that chinning and chesting are causally linked with a state of arousal arising from social stimuli. Thus an increase in female marking when a joey has started to leave its mother's back may be the result of an increased arousal caused by interactions with her joey. Observations of chinning and chesting performed when a joey was actually following its mother coincided with the onset of other aggressive behaviour by the female (Fig. 5.29).

At about 180 days a group of female aggressive behaviours consisting of the head turn, raised paw and fight were observed to occur for the first time (Fig. 5.29). They developed at the time when the joey was still spending a significant proportion of time on its mother's back. They are little more than incipient threats (the shrug is of the same type), but may at times lead to actual striking or biting. Some of the threat postures were given when a female was involved in an agonistic interaction with another adult, and were apparently a result of the female briefly mistaking the identity of her joey. However, others were

undoubtedly directed at her joey and as early as 181 days were functional in the sense that the joey was prevented from climbing onto its mother's back. It is significant that no submissive behaviour by the joey is observed in these interactions. This implies that a young joey does not recognise the threatening signal incorporated in a raised paw or a quickly turned head. An implication borne out by the early occurrence of actual biting and striking when a female wishes to prevent her joey climbing onto her back.

After about 210 days a series of both female aggressive and joey submissive behaviour patterns develop, with urine and cloacal marking being the last (Fig. 5.29). It is the development of submissive behaviour by the joey which is the most significant feature of this series. A joey has begun to recognise the female's potential for aggression, clearly apparent when the joey gives way to,or cautiously approaches its mother, even when the female may not be acting in an overtly aggressive manner towards her joey. Also a chase is not possible without the reciprocal action of rapid withdrawal, otherwise it becomes a fight, and a direct stare or other form of threat only becomes effective when the individual at whom it is directed recognises it as a threat.

In the development of agonistic behaviour two main phases can be recognised. First to develop is the group of behaviours consisting of incipient threats and actual contact agonistic encounters, but without any parallel development of joey's submissive behaviour (Type I). Secondly there is the group which is characterised by the presence of submissive behaviour by the joey (Type II).

Olfactory behaviour could not be fitted into either of the above types because of the complete lack of observable response by the joey to scent marking. Chinning and chesting develop at the same stage as the Type I, whereas urine and cloacal marking come late in Type II agonistic behaviour. Olfactory marking is not in itself aggressive in the sense that a raised paw is, because the scent itself does not contain any direct deterrent. Rather its function will be derived from behaviour associated

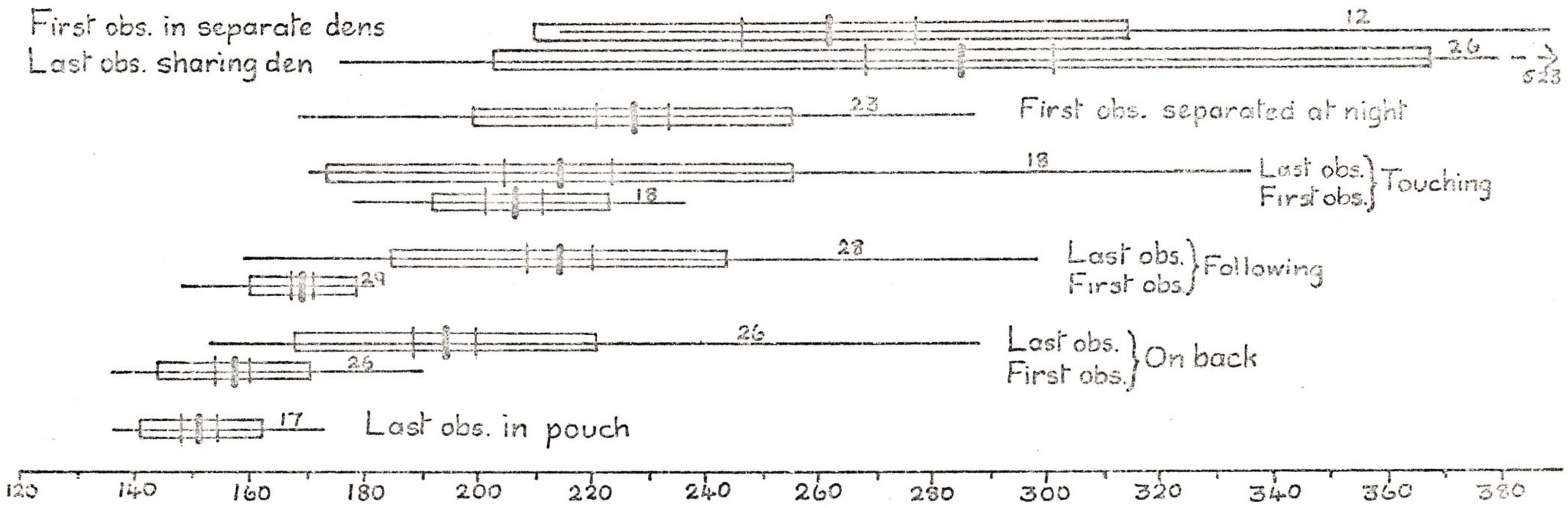


Figure 5.30 : Observed distribution of mother-joey behaviour in relation to age of joey.
Mean = broad vertical bar; standard error = narrow vertical bars;
standard deviation = box; range = horizontal line; sample size = no. on line.

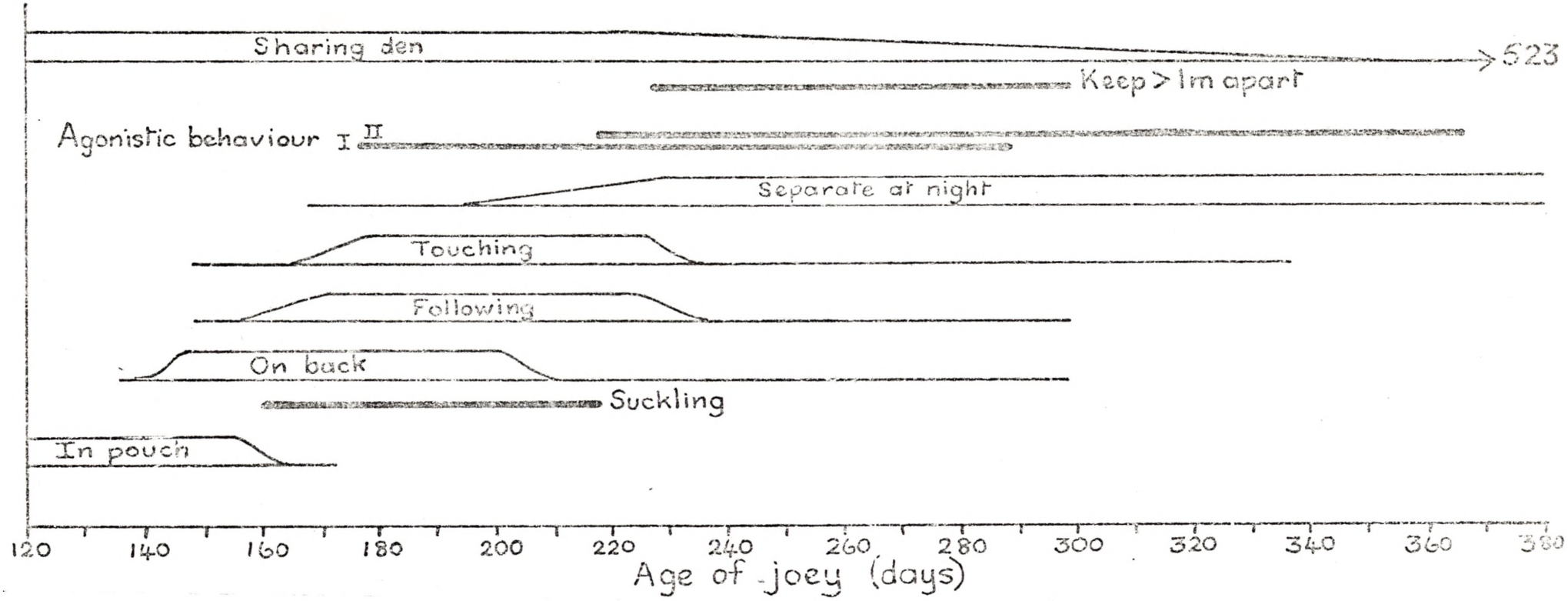


Figure 5.31 : Adjusted distribution (see text) of mother-joey behaviour in relation to age of joey. Horizontal line = actual range; depth = proportion of joeys considered to be exhibiting the behaviour.

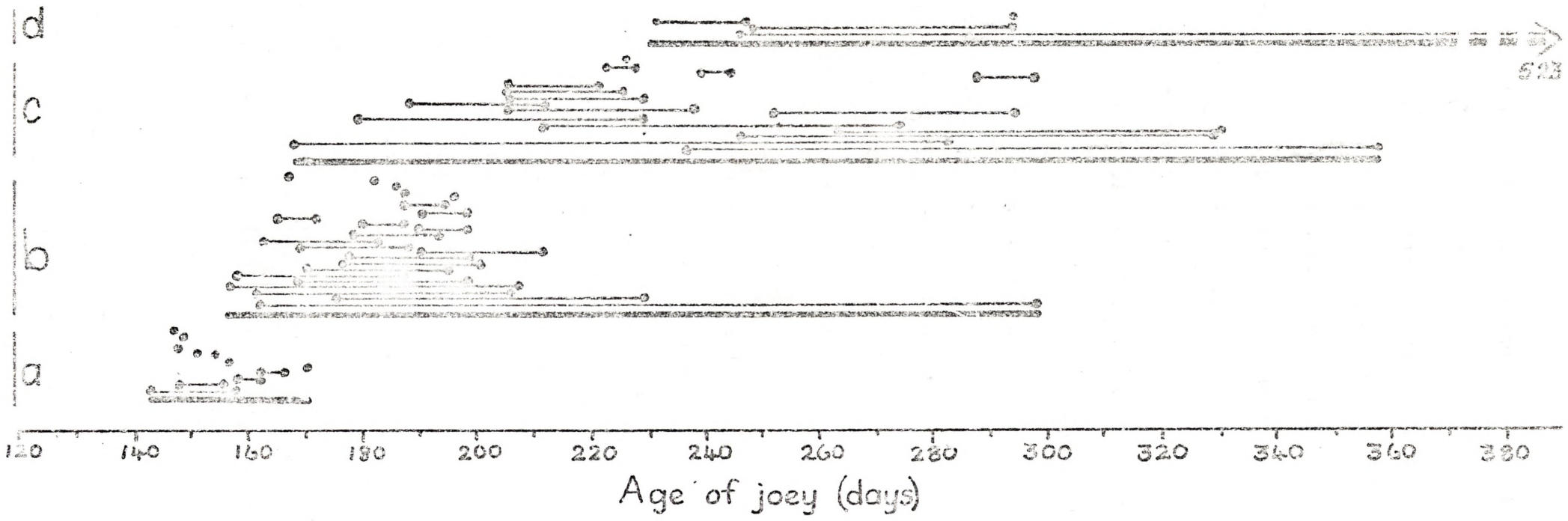


Figure 5.32 : Overlap of mother-joey behaviour for individual pairs. Overlap between a) entering pouch and riding on back, b) riding on back and following, c) following and joey separated from mother at night, d) sharing maternal den and using separate dens; dots = first and last obs of overlapping behaviour for individual pairs; heavy line = range of overlap of all individual pairs.

with it. With chinning and chesting developing at an early stage in the mother-joey relationship, when cohesive behaviours are common (see next section) it is possible that it may function as a cohesive signal as suggested by Bolliger & Hardy (1944). However, with the onset of agonistic behaviour of both types I and II and from the observed contexts within which chinning and chesting occurred, it probably becomes associated more with aggressive behaviour. With cloacal and urine marking, all observations occurred in an agonistic context, and with its later development it suggests that this type of olfactory marking is more aggressive than chinning and chesting.

5.617 Development of mother-joey relationship

In the present study the development of the mother-joey relationship is based on the first and last records of various behaviours observed in the field (Fig. 5.30). However, because of the irregular nature of observations on individuals the statistical mean for either the first or last record of a particular behaviour will be skewed either towards a younger age for the last record of an event and vice versa for the first. For example the last record of a joey seen in the pouch cannot be made after, but can be made before a joey has ceased to use the pouch. Thus the mean of such observations must occur at a younger age than the true mean, unless the mothers and their joeys were kept under constant surveillance, an ideal far from reached in the present study. Similarly the observed mean for first observations of a joey on its mother's back must occur at an older age than the mean. In the construction of Figure 5.31 therefore, an attempt has been made to reduce the above flaw by adjusting the beginning and end of a stage to a position which in my opinion represents a truer picture than the purely statistical one obtained in Figure 5.30. Consecutive stages overlap each other, and this overlap for individual mother-joey pairs is shown in Figure 5.32. Again the observed overlapping time for individual pairs is bound to be less than the true time, whereas the range of all pairs will almost certainly be greater than for any one pair.

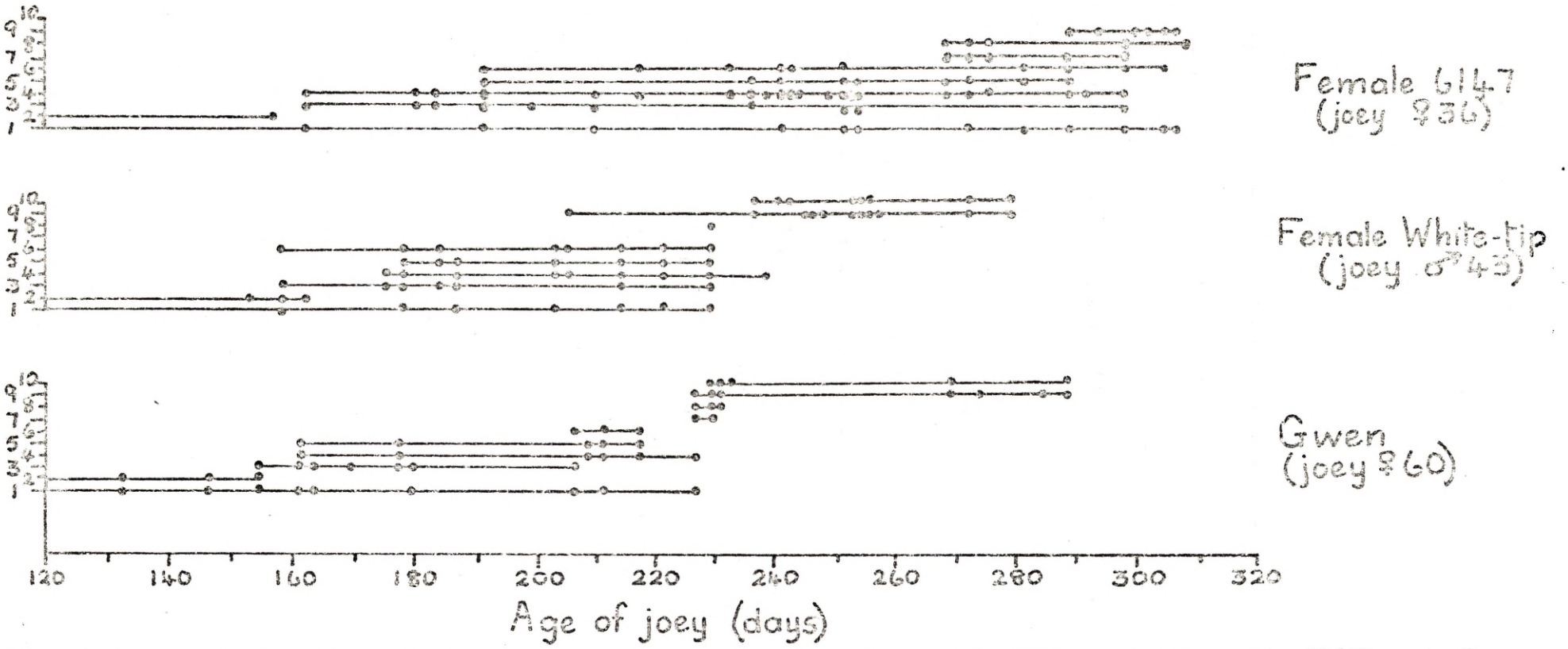


Figure 5.33 : Distribution of mother-joey behaviour in relation to age of joey, for three individual pairs. Dots = obs; horizontal line = range.

1 = sharing den
2 = in pouch
3 = on back
4 = following mother when away from den
5 = approaches within 1m of mother away from den
6 = touching
7 = keeps more than 1m from mother
8 = agonistic behaviour
9 = travelling independently away from den
10 = using separate dens

The following developmental pattern occurs, based on Figure 5.31. For approximately 15 to 20 days a joey will both ride on its mother's back and enter the pouch, but by the age of 160 days it has ceased to enter the pouch. The end of entering the pouch coincides fairly closely with the onset of following its mother, an important step in that it represents the departure from actual bodily contact with its mother, and emphasised by the relative lack of observations of a joey both following and in the pouch on the same night (2 obs age of both joeys 157 days). Although at the age of 160 days there is the change from a complete bodily contact relationship to one where bodily contact begins to be broken, it is not a sudden or total change because contact behaviour in the form of back riding, suckling and touching continues. Away from the den most joeys cease to ride on their mother's back between the age of about 200 to 210 days and this coincides approximately with the onset of a joey beginning to travel independently at night though still sharing a den. Nevertheless contact behaviour in the form of touching continues for another 20 to 30 days, when by the age of about 230 days most joeys have ceased contact behaviour with their mother, which coincides with the end of following behaviour, and with the onset of the use of separate dens by some joeys. In the vicinity of the den contact behaviour may continue beyond 230 days. Agonistic behaviour Type I begins while a joey is still riding on its mother's back, and agonistic behaviour II begins between 210 and 230 days, at about the time back riding ceases.

Thus there appears to be three important stages in the development of the mother-joey relationship. First at about 160 days when actual body contact begins to diminish, but a joey continues to keep close to its mother; secondly between 200 and 220 days when most joeys will have started to travel independently at night while still sharing the mother's den; thirdly at about 230 days when contact behaviour ceases, at least away from the den tree, and dispersive behaviours appear.

As examples of individual mother-joey relationships the three best documented case histories are given and summarised in Figure 5.33.

Case history 1 : Gwen and joey, Female 60 (Fig. 5.33a)

Up to the age of 217 days the relationship was typically a contact one with the joey coming within 1m of its mother when following, and still sitting touching her at times, and with no sign of any dispersive behaviour.

By the age of 226 days however there had been a marked change. Both Gwen and her joey came out of the same den at dusk and remained at the den entrance touching for 8 min. When Gwen moved away from the den her joey did not follow until 6-8 min later, and when it did there appeared to have been a distinct change in its behaviour. The joey approached its mother but stopped 1m away with Gwen staring at it. It then turned and moved back to 4-5m. In the next half hour before Gwen left the den tree her joey approached once more but again stopped 1m from her, and hurriedly retreated when the female turned to look towards it. When Gwen came down the tree her joey gave-way in front of her.

Three nights later mother and joey came out of separate dens in the same tree. Gwen took no apparent notice of her joey, but the joey watched its mother closely while they were both in the den tree and never came closer than 2m. On the following night they again came out of separate dens in the same tree and appeared to completely ignore each other, and the joey made no attempt to follow its mother when she left the den tree. At dawn her joey was already in the den tree when Gwen returned, and following a give-way interaction in which Gwen supplanted her joey they entered separate dens.

The next observation was 39 days later when the joey was 269 days old. By then the joey had left the maternal den tree and was using a den in a separate tree, and the mother-joey bond appeared to have completely broken down.

Case history 2 : Female White-tip and joey, Male 43 (Fig. 5.33b).

Up to the age of 229 days the joey maintained a predominantly contact relationship with its mother although it had begun to travel independently of her by 205 days. At 229 days the first signs of female aggression appeared, it being a light chinning of a branch as her joey followed her.

Between the age of 229 and 236 days there was a marked change in the relationship similar to that observed in case history 1. At 236 days Female White-tip and her joey emerged from dens in separate trees about 75m apart and neither made any attempt to join the other when they came down to the ground. Two nights later (238 days) they were seen in the same tree, not a den tree, 4m apart but I did not stop to watch them. At 240 days Female White-tip emerged from a den unaccompanied by her joey, and at 242 days they emerged from separate dens in the same tree, the joey's den being 2m off the ground and about 15m below its mother's den. The joey left the tree within minutes of emerging without any attempt to join its mother.

The last observation of the joey was at 279 days when it, and its mother were seen emerging from separate den trees. It was not seen again although observations continued in tha area for at least another month. Either it had left its mother's home range completely or had died.

Case History 3 : Female 6147 and joey, Female 36 (Fig. 5.33c)

Unlike the preceding two cases Female 6147's joey maintained a contact relationship with her right to the end of the series of observations which ended when the joey was 307 days old. Nevertheless between the age of 253 and 268 days there was a definite change in the relationship.

Up to 253 days the joey had a predominantly contact relationship with its mother, without any agonistic behaviour. This was similar to the contact relationships in the previous two case

histories except that it had continued for 20 to 30 days longer. By 268 days however both female aggression and joey submissive behaviour had developed, and once away from the den tree the relationship was no longer a contact one as Female 6147 would not allow her joey to come within 1m of her.

Figure 5.33c shows a considerable overlap between cohesive and dispersive behaviours, this being the result of the difference in behaviour when in the den tree and when away from it. A good example of this change in behaviour when mother and joey moved away from the den tree are the observations when joey was 298 days old. After coming out of the den Female 6147 and her joey sat at the entrance, with the joey behind, and half on its mother's back for 9 minutes. The female then moved 3m further up the tree, and the joey followed a little later to sit within 15cm of its mother without any sign of agonistic behaviour. A minute later the female crossed into a contiguous tree and sat grooming about 2.5m from her joey who did not follow. Twenty two minutes after emerging from the den Female 6147 began to move down the tree prior to leaving it. Her joey, who had been moving about in the den tree, crossed to the other tree and followed its mother. It was at this stage that the behaviour of both female and joey changed. As the female moved down the branch she lightly marked it with her cloaca, and although the joey took no apparent notice of the olfactory mark it watched her intently as it followed and stopped 2m above her, and when the female looked up at her joey it immediately turned and retreated 1m. Almost immediately the joey turned and again approached its mother cautiously but stopped 2.5m from her ready for instant flight. When the female started to move on down the tree, her joey retreated up the branch even though the female had made no apparent aggressive move towards it, then followed keeping 2-3m behind. Once during a pause the female approached her joey from behind and gently bit it on the rump at which the joey hurriedly moved away 1m. On the ground

the joey continued to follow, keeping about 3m behind its mother. Once the female chased her joey briefly, and a little later there was a brief scuffle. About 1 hr after emerging from the den, they began to drift apart as they fed on the ground and went up separate trees 10m apart.

It was the switch from amicable, or at least neutral behaviour, in the den tree to mild aggression by the female and distinct submissive behaviour by the joey away from the den tree, that was the most striking feature of this observation. In terms of spacing this was expressed as a switch from a contact relationship in the den tree to a non-contact one away from the tree, with the joey coming no closer than 1m to its mother except at contact agonistic encounters.

Almost identical behaviour occurred at 268 and 272 days with agonistic behaviour becoming apparent once they moved from the den tree into the contiguous tree prior to coming down to the ground. As shown in the traces in Figure 5.24 there was the corresponding change in distance with the joey coming no closer than 1m.

It was not necessarily the act of actually leaving the den tree which triggered the change in the relationship. At 288 days Female 6147 came down the den tree to the ground instead of crossing into the contiguous tree first. As she moved down the tree she gave the series of grunts and screeches previously described in the section on auditory agonistic behaviour. Thus agonistic behaviour may begin when mother and joey are leaving the vicinity of the den irrespective of whether they are still in the den tree.

The gradual change in the relationship between Female 6147 and her joey was emphasised by the observation at 281 days (joey's age). For the first hour they sat at the den entrance, much of the time touching. When the female did move away from the den she came straight down the tree closely followed by her joey who kept within 1m of her, with no sign of agonistic behaviour. When the female

came down to the ground and crossed to another tree, the joey paused about 1 min before following, climbed into the same tree and both began feeding. Throughout the 90 min of observations there was a complete lack of any sign of agonistic behaviour by either mother or joey, unlike observations which had taken place on earlier nights when the joey was 268 and 272 days old.

In the three case histories given, two types of relationship occurred. One in which there was a sudden and virtually complete breakdown of the mother-joey relationship as shown by the first two. The other in which there was a definite change, in that away from the den the relationship became predominantly a non-contact one with agonistic behaviour, but in the vicinity of the den it continued to be a contact one. Thus, although the relationship had changed, the bond was still maintained in the vicinity of the den.

Other mother-joey relationships were not as well documented as the above three, but in a further 13 cases it was possible to determine whether the change in the relationship was an abrupt breakdown or whether it was a more gradual change. This was based on the assumption that the continued sharing of the den after the development of dispersive type behaviours was indicative of a gradual change. From the records of individual relationships all those classified as gradual were known to be still sharing a den after the age of 280 days. Of the 16 relationships thus classified, significantly more were of the gradual type, with the sex of the joey having no significant effect (Table 5.42).

Table 5.42

Type of breakdown of the mother-joey relationship tested for, a) independence with sex of joey, and b) parity of abrupt : gradual ratio.

		Breakdown		
		Abrupt	Gradual	Total
Sex of joey	Male	1	4	5
	Female	3	8	11
	Total	4	12	16

a) G (type of breakdown : sex of joey) = 0.096 1 d.f. $p > .5$

b) G (abrupt : gradual parity) = 4.186 1 d.f. $p < .05$+

5.618 Ontogeny of feeding behaviour

Suckling behaviour was observed to continue up to the age of 217 days, and this may be true suckling because females were known to lactate up to 238 days, nor was any female observed to have finished lactating before 220 days (Fig. 5.27).

A joey will begin to take solid food long before suckling ceases as the youngest seen to do so was 154 days old, which is 18 days after the earliest observation of a joey out of the pouch.

Three observations were made of joeys feeding from their mother's back. Presumably this is how a joey begins to sample leaves even though the earliest observation of a feeding joey occurred when it was off its mother's back (Fig. 5.27). In all three observations the female was herself feeding when her joey on her back also began to feed. When feeding from its mother's back a joey did not reach out to grasp the leaf with its front paw (both of which continued to tightly grip the female) but merely lent towards the leaf to take it into its mouth.

The earliest observation of a joey feeding (age 154 days) occurred when Gert had "left" her very young joey on the other side of the tree. Whilst sitting waiting for its mother the joey once reached out with its left front paw and pulled a leaf towards its mouth. However, I was unable to see whether it actually ate the leaf. Although this observation may have been only very brief sampling, in the next observation a joey of 157 days was feeding steadily on eucalypt leaves.

There was no evidence that a mother actively encouraged her joey to start feeding. However, social facilitation probably is largely responsible, because in all three observations of joeys feeding from their mother's back, the female was also feeding. Eleven observations of joeys feeding when not on their mother's back were made up to the age of 181 days. In seven the joey did not start to feed until its mother had begun, in two the mother was merely sitting when the joey began feeding, one was the observation of the youngest joey sampling a leaf, and in the eleventh the activity of the female was unknown.

A young joey can learn new foods from its mother, because the semi-tame female at Tyne St. would allow her joeys to take pieces of bread, apple etc. from her paws, without any sign of agonistic behaviour. However, some time after they had ceased to ride on her back the female prevented her joeys from taking food from her.

5.62 Adult Female - Juvenile (other than own) Interactions

The number of observed interactions between an adult female and a juvenile which was not her own was low. Only four were observed when the juvenile (6 to 8 months old) was in the vicinity of its mother. Two either preceded or followed interactions between the adult females. Following a chase and fight between Jess and Jill, Jill's 196 day old joey was separated from its mother with Jess between them and 2m below the joey. The joey gradually crept down the branch in an attempt to bypass Jess and get to its mother. When about 0.6m away Jess moved towards the joey and there was a brief aggressive encounter followed by the joey shooting back up to its original perch. The second time the joey crept down the branch it drew level with Jess and within 0.5m of her but then retreated once again. In the second observation Eve first chased Iena's 209 day old joey then Iena.

In the other two observations there was no interaction between the females. In one Eve's 211 day old joey hurriedly returned to its mother, 3m away, when Jill climbed the tree towards them. The fourth interaction observed occurred when Jill, followed by her 169 day old joey, gradually moved towards Jess as they all fed on the ground six hours after the interaction described above. When within about 5m of each other Jill began to travel at a steady pace away from the area. I watched Jill but when I noticed that her joey was not following her I found it still 3m from Jess. It was half crouched on the ground looking directly at Jess who was apparently taking no notice of the joey. The joey remained perfectly still, staring at Jess even after the female had moved away, and in fact it remained in this position 3-4min after Jess had left before it relaxed and began to move away itself.

Three of the above observations, especially the last, indicate that

a joey can distinguish between its mother and another female, although how it does this is not known. This recognition may partly depend on the orientation of the females rather than an ability of the joey to recognise individuals per se, especially since joeys may apparently follow males mistaking them for their mothers (see Ch. 5.71).

Four interactions were observed when the juvenile (in all 4 a female) was travelling independently of its mother or after the break-down of the mother-joey bond. In three the adult female chased the younger female who ranged in age from 10 to 14 months, twice from a den tree in territorial interactions. In the third Eve crossed into the same tree as Jess (10 months) and approached her. There was a short chase followed by a brief scuffle accompanied by a brief chatter. Jess broke away but instead of a chase developing they froze about 0.5m apart, the younger female facing up the tree and broad side to the older female who was hanging head down diagonally facing the other. After holding this position for two minutes the younger female began to move away and immediately the older female started a chase. In the fourth interaction observed a 10 month old female watched an adult female climb into the same tree and when 4-5m away the juvenile hurriedly crossed over into the next tree.

All four were agonistic interactions, at a time when the young female was attempting to establish a home range of her own. The fact that 3 out of the 4 interactions were chases, one with an accompanying scuffle, suggests that the level of antagonism of an adult female towards a female joey of this age is relatively high.

Two adult females that I kept in captivity in New Zealand shared a nest box, and both had pouch joeys, one slightly older than the other. At the time that the older joey was just beginning to leave the pouch, it was found on one occasion, not in its own pouch, but sharing the pouch of the younger joey. The significance of this observation awaits further study, but does indicate that a female brush-tail possum does not automatically reject a strange joey.

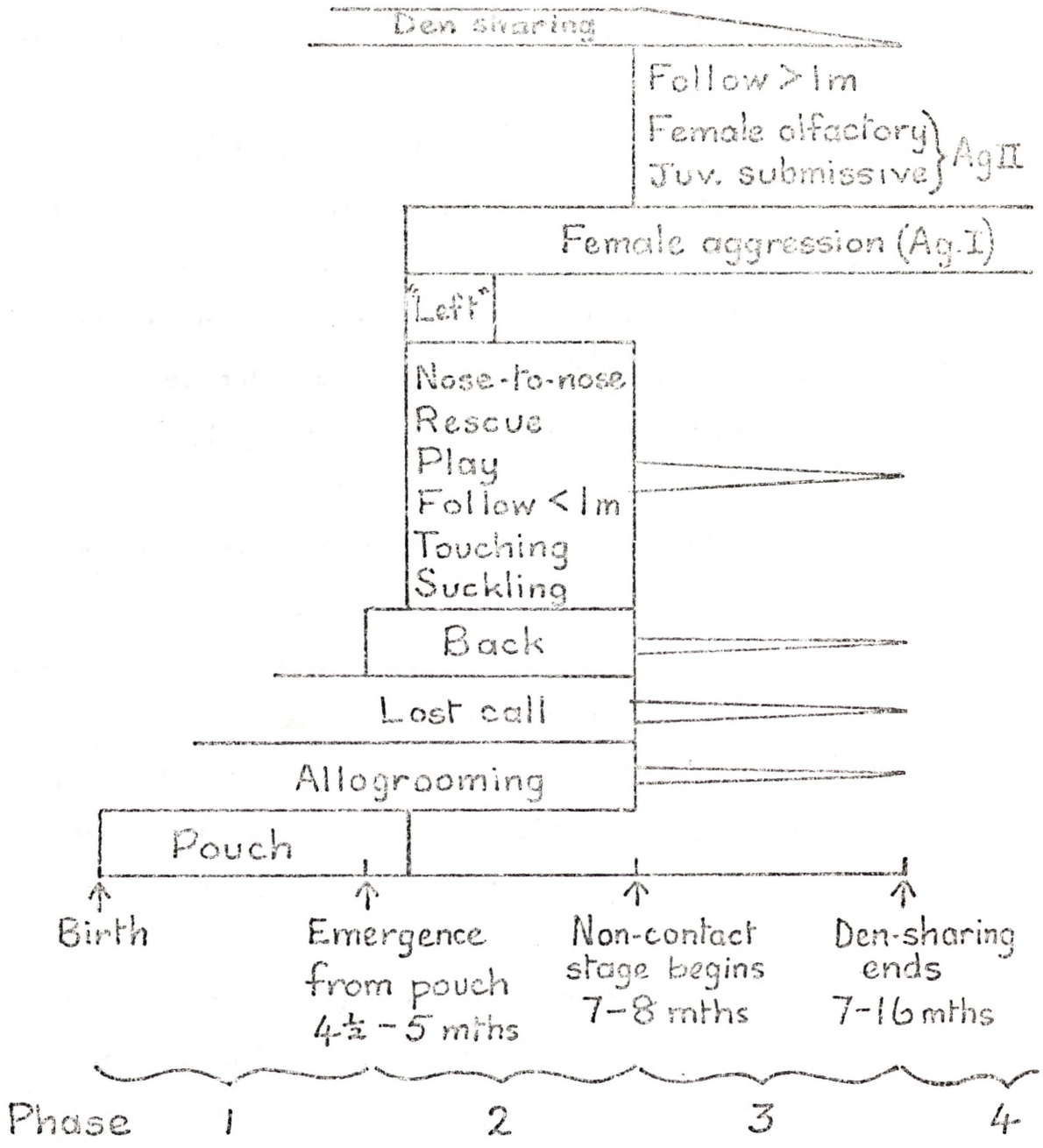


Figure 5.34 : Schematic diagram of mother-joey relationships.

5.63 Discussion

Social development of the young brush-tail possum is summarised in the schematic Figure 5.34, which is an interpretation of the data presented previously.

Three phases from birth to independence are recognised.

Phase 1 is from birth to the emergence of the joey from the pouch 4.5 to 5 months later. Social development can be said to have started from the time that the embryonic-like joey makes the journey from the cloaca to the pouch, with no positive help from its mother except that she squats on her haunches (Lyne, Pilton, and Sharman 1959).

During the pouch stage, social behaviour between mother and young is probably limited to bouts of licking by the mother when she cleans out the pouch. The young possum is capable of vocalising while still confined to the pouch but was heard only when actually handled. However, this study was not concerned with this phase in the social development so it is not known what responses the mother gives to the pouch young. Russell (1973) has studied mother-young behaviour in two macropods in more detail, and the only responses observed by the mother were limited to comfort movements.

Phase 2 begins with the emergence of the joey from the pouch and continues until the mother-joey bond ceases to be a contact one away from the den. This phase is characterised by contact behaviour and the most conspicuous maternal behaviour. Leaving the shelter of the pouch is an important step for both joey and mother as the risk of becoming fatally separated obviously becomes much greater. The joey remains in constant contact with its mother, clinging to her back or pressing against her. As the joey's confidence increases it begins to make tentative forays away from its mother, at first keeping within 1m, then extending this to 3-5m when the female is feeding, and finally travelling independently at night. Throughout this phase the joey returns to its mother at irregular intervals during the night, apparently as a form of reassurance behaviour. It may either walk right up to its mother then away again, or

climb onto her back, for varying periods of time, especially if disturbed. Apart from back riding, other forms of contact behaviour are "suckling" and touching.

Maintaining proximity appears to be primarily the concern of the joey. It keeps a close watch on its mother and follows her, early in the phase whenever she makes a move, but later only if she moves out of a particular branching system and there is a danger that the joey may be left behind. The mother has no form of cohesive vocalisation and does not approach her joey before moving away. The only concession the mother makes is to pause after she has begun to move away, or to wait if the joey falls too far behind, so that the joey can catch up with her. If the joey is unable to keep up with her the mother will return to it, though not necessarily at once. The "leaving" of young in trees away from the den may arise in situations where the joey is unable to follow its mother. In interactions between a joey and a male the mother reacts more positively by coming to the joey's aid.

The mother begins to show aggressive behaviour towards her joey during phase 2. At the beginning of the phase the aggression may consist of little more than slight intention movements, but by the end actual biting and hitting may take place. However, there is no obvious concurrent development of submissive behaviour by the joey until right at the end of the phase. The rudimentary "play" observed may represent a learning stage of agonistic behaviour.

Phase 3 begins when the mother no longer allows her joey to approach within 1m when away from the den tree. This phase is characterised by the appearance of obvious joey submissive behaviour, and by an increase in, if not the actual onset of, female olfactory marking. In the immediate vicinity of the den a contact relationship typical of phase 2 may continue, possibly with the waning of contact and cohesive behaviour. The ending of phase 3 and the onset of complete independence occurs when the maternal den is no longer shared. In those cases where an abrupt breakdown of the mother-joey bond occurred, the beginning of phase 3 coincided with the

joey leaving the maternal den, so, in effect, phase 3 was omitted. In other cases den sharing could continue up to the age of 16 months.

Phase 2 is probably the most critical in the development of the young possum. It allows the joey to become progressively more independent and more familiar with the maternal home range, yet at the same time retain the security of the maternal den and the protection of its mother, so that when the contact phase of the mother-joey bond ceases it is sufficiently independent to fend for itself. Phase 3 allows the development of independence to proceed even further while still based on the security of the maternal den, thereby increasing the probability of the young's success in establishing its own home range.

A number of features in the mother-joey relationship of the brush-tail possum appear to be general to marsupials. One is the relative unconcern of the mother towards her young. Kaufmann (1974) describes whiptail wallaby mothers as "...not very solicitous or protective towards their young once they leave the pouch.", and Russell (1973) remarks on the "....relatively passive role of the mother in the relationship..." in both the Tamar wallaby (Macropus eugenii) and the red kangaroo (Megaleia rufa). In the dasyurid Sminthopsis crassicaudata both the young and the female treat each other with equal indifference once the young have begun to leave the nest (Ewer 1968b).

Allowing for this apparrent indifference of marsupial mothers to their young, some do show protective behaviour. The most pronounced protective behaviour is exhibited by Sminthopsis crassicaudata with the female displaying overt threat to both conspecifics and disturbances by an observer, especially when the young are being left in the nest (Ewer 1968b). Sminthopsis crassicaudata has an immobile litter in a nest to protect, whereas neither the above macropods nor the brush-tail possum show such pronounced defence, probably relying more on flight as a defence mechanism. Also related to the possession of an immobile nest is the retrieval of young by Sminthopsis crassicaudata and another dasyurid Dasycercus (Ewer 1968b), and a didelphid, Marmosa cinerea,

(Beach 1979, quoted in Ewer 1968b).

In the macropods the female red kangaroo responds to the lost call of its young with a soft vocalisation (Russell 1973), whereas the whiptail wallaby reacts with indifference to its young in distress during agonistic interactions with other adults (Kaufmann 1974), and in fact Kaufmann makes no reference to any juvenile distress vocalisations. The differences between the two macropods can possibly be correlated with the mean size of the group which is 2.5 in the red kangaroo (Caughley 1964), and 6 in the whiptail wallaby which is a sub group of a larger "mob" (Kaufmann 1974). It may be more imperative that the young stays closer to its mother in the more solitary red kangaroo, hence both the joey lost call and the answering call by the mother. The brush-tail possum has three forms of the joey lost call but no vocal response from the mother. Instead the mother's response is to return to her joey. If her return is not immediate the joey, especially early in phase 2, remains in the one place. In an arboreal mammal it makes sense that it is the mother who returns to the joey when it is lost, because the mother will know the route through the complexity of branches. This may explain the well developed lost call by the young and the lack of vocal response by the mother. The ring-tail possum (Pseudocheirus peregrinus) produces a "...high pitched chirrupping twitter which can almost always be heard if undisturbed possums are observed while moving about and feeding at night. The same call, repeated at fairly regular intervals, is also used by juveniles of post-pouch age which have become separated from their mother." (Thompson and Owen 1964). The common ring-tail has an average litter size of two (Thompson and Owen 1964), and although the function of the twittering is not known, it may act as a contact call between mother and young. With two young to be looked after one may expect that young ringtails need to keep much closer to their mother than young brush-tails, or else that litter mates would remain very close to each other.

The most immediate and obvious protective response of the brush-tail

possum was to go to her joey's aid when it had an agonistic interaction with a male. Males were never observed to actually attack a dependent juvenile, but the possibility of serious injury to the juvenile should an interaction develop into a fight may account for the mother's definite reaction. In other contexts the reaction of the mother was no so definite. A ring-tail possum has been known to actually attack an observer handling her young (Marsh 1967), but in the brush-tail possum this possibility seems remote.

Closely related to the marsupial mother's indifference to her young, is the primary role played by the young in keeping up with its mother. Neither Kaufmann (1974), nor Russell (1973) were able to detect any behaviour which they could construe as the mother being responsible for maintaining proximity with her young. Only after a detailed study of the brush-tail possum was it appreciated that subtle behaviour such as a pause, or actual waiting by the mother allowed the joey to keep up with her.

The change from phase 2 to phase 3 in the mother-joey relationship of the brush-tail possum may have its equivalent in the whiptail wallaby which shows a sharp increase in the independence of the young a few months after leaving the pouch (Kaufmann 1974). However, this was apparently not correlated with any increase in the aggressive behaviour of the female as it was in the brushtail. Possibly this stage in the whiptail is more the equivalent of phase 3 in the brush-tail when the maternal den is no longer shared. Russell (1973) mentions no such change in behaviour of either the Tamar wallaby or the red kangaroo, but her studies were concerned more with the earlier stages of the young and its mother.

Until further detailed studies on marsupial mother-young relations are made it is still uncertain which of the behaviour patterns of the brush-tail possum are characteristic of marsupials in general, or are specific to the possum.

5.7 ADULT MALE-JUVENILE RELATIONSHIPS

The first interactions between an adult male and a juvenile were

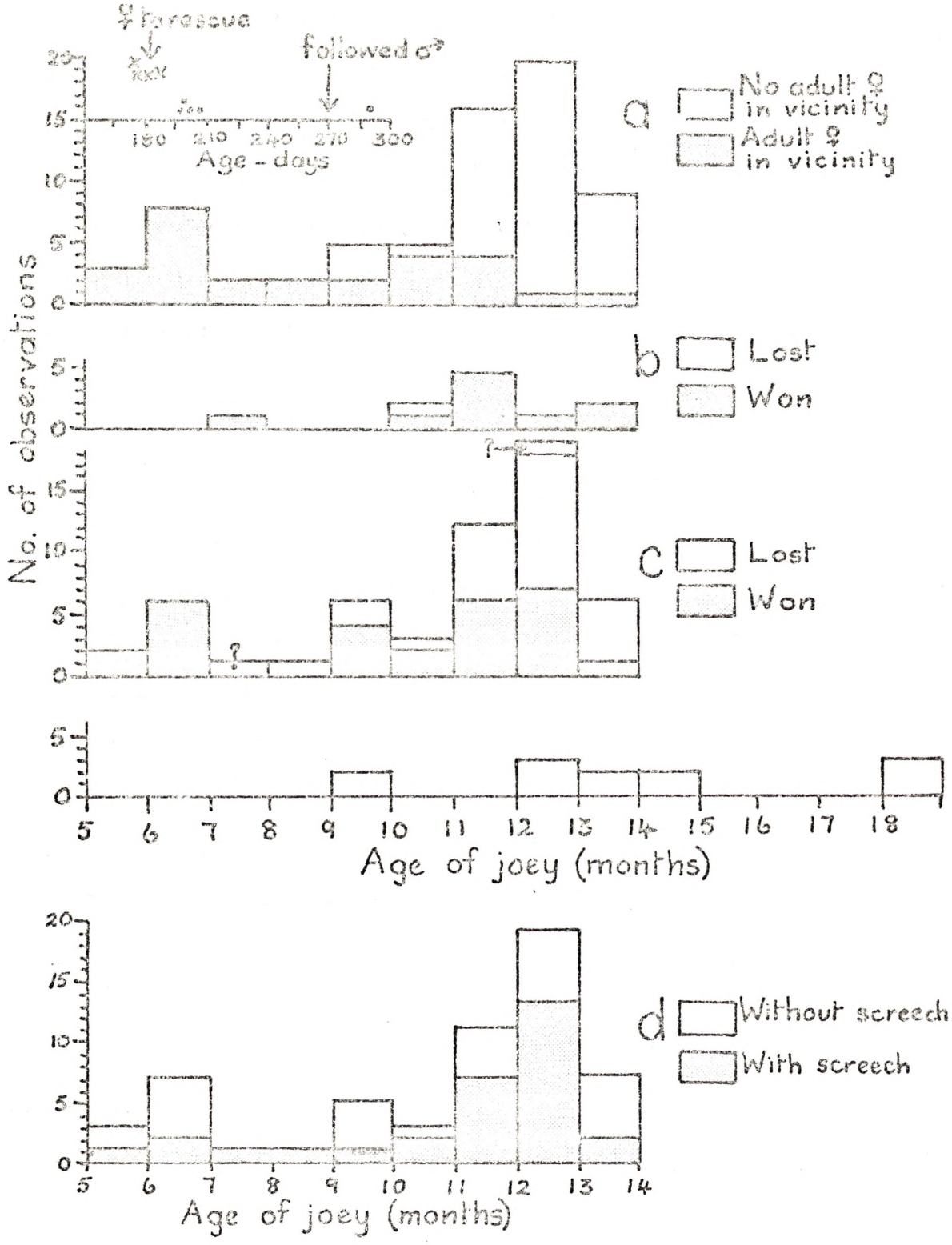


Figure 5.35 : Adult male - juvenile interactions in relation to age of juveniles.
a) interactions in vicinity of adult female.
b) winner of adult male-juvenile male interactions.
c) winner of adult male-juvenile female interactions.
d) first known conception of juvenile female - interred from known births.
e) juvenile female interactions accompanied by screech.

observed to occur when a male became sexually attracted to the juvenile's mother at the time when the juvenile was beginning to leave the pouch. Up to the age of eight months all male-juvenile interactions observed took place in the vicinity of an adult female (invariably the juvenile's mother). From eight months on an increasing proportion of interactions took place away from a female (fig. 5.35). This is indicative of the increasing independence of the joey from its mother, and of an increasing interest in the juvenile itself by the male.

5.71 Interactions with young juveniles

Joeys seven months or younger were obviously nervous of a male when he approached their mother or stayed in her vicinity. For example Jill's 177 day old joey climbed onto its mother's back 14 times during one 90 min observation period, which was an unusually high number of times. This was attributed to the presence of Male 32 within 6m of Jill. The joey made repeated sorties of about 1m from its mother, but would almost immediately return and either sit very close to her or climb onto her back. At one stage Jill crossed a gap and her joey was unable to follow, but she returned to her joey hurriedly when it approached Male 32. Jill then chased Male 32 a number of times, and each time her joey ran after her and attempted to climb onto her back, sometimes successfully. Towards the end Male 32 came within 1m of Jill, and by this time the joey was sitting half under its mother with its head tucked into the pouch region.

A male's reaction to a joey accompanying its mother was usually one of indifference. In one mating sequence a joey of unknown age was on its mother's back when a male mounted. He merely pushed the joey to one side without any apparent aggressive behaviour until it attempted to clamber over its mother's shoulders onto her back, and the male then bit at the joey which made it hurriedly swing under the branch under the female. As the male was pelvic thrusting the joey attempted to enter the pouch from behind between its mother's legs. Eve's 199 day old joey reacted to the approach of Don by rapidly withdrawing 2-3m further up the tree. Don took no apparent notice of the joey and immediately mounted and mated with Eve.

However, after mating he did climb the tree towards the joey, whereupon it screeched, bringing its mother to its rescue.

When a young juvenile met a male it either withdrew rapidly or gave a screech which brought its mother to its rescue. A female was observed to respond in this way to joeys up to the age of 177 days (Fig. 5.16).

Twice when a joey was following its mother a male approached from behind and to one side of the female and cut in between the mother and the joey in order to follow the female. The joey's only response was to drop back and to follow the male who in turn was following the female.

On five occasions a joey followed a male apparently mistaking it for its mother. Four of these involved 6 month old joeys (199, 199, 203 and 208 days of age) of four different females. The clearest example occurred when Male 32 and Jill, with her 208 day old joey, came out of dens in the same tree. Just before Male 32 came down the tree the juvenile was only about 2m above him and the female was about 6m above the juvenile. Male 32 came rapidly down the tree and jumped to the ground. The juvenile did not follow immediately, in fact not until the male was about 12m below it, but when it did it came rapidly down the tree and bounded over the ground after the male. Male 32 sat up and looked towards the juvenile who had stopped 6m away. The juvenile then approached to within 3m before making an alarm dash into a nearby tree. However, it came down onto the ground and approached to about 1.25m of Male 32 who was just sitting looking back over his shoulder at the juvenile. For the next 3-4min they fed on the ground keeping within 3m of each other. Male 32 appeared to ignore the juvenile, which kept looking up towards him as though uncertain about him; perhaps it had realised that it had not followed its mother. When male 32 trotted away the juvenile bounded after him for a short distance to continue feeding 3m from him. Eventually after they had been on the ground for approximately 7 mins the juvenile made a series of six alarm leaps, one after the other, heading back towards the den tree, before finally climbing a tree 52m from the den tree. It was not apparent whether this series of alarm leaps was associated with the male or had

some other cause. Throughout this Jill had remained in the den tree, apparently completely unconcerned for her joey, although she did join it in its tree later.

In the remaining three observations the interaction was relatively brief. For instance when Gert began to climb a tree, followed by her 203 day old joey, Gus hurriedly came down the tree past them and the joey jumped to the ground, bounded after Gus and leapt onto the trunk of a tree beside him. When Gus climbed the tree, however, the joey, who by this time was back on the ground, remained at the base of the tree for 5 min frequently looking up the tree, as though trying to decide whether to climb it or not.

It did jump back onto the base, as though to climb the tree, but turned round and came back down to the ground. In another observation Don and Eve's 199 day old joey were about 0.6m apart and 3m above Eve. Don then moved away to cross into the adjacent tree and passed about 0.3m from the joey. There was no agonistic behaviour and the joey followed Don across into the next tree down the branch to the main trunk then up the trunk, a distance of 6-9m. They then began to feed about 4.5m apart. In the fourth observation Alice's 199 day old juvenile climbed into a tree containing its mother, Male 32, and Alec. The juvenile climbed to the lowest crotch and looked up at Alec who was the lowest of the other three possums. It moved towards him and appeared to be trying to catch up with him as he moved higher in the tree. They stopped with the joey 0.6m behind. Alec turned and approached the joey, without any sign of overt aggression, who in turn gave way.

One other example of a joey following a male apparently mistaking it for its mother occurred with an appreciably older joey (288 days). Female 6147's juvenile was still following its mother despite its age (see previous section), and on this occasion it approached Male 9. The male rapidly gave way, stopped to look round at the juvenile then once more gave way. The juvenile in the meantime continued to follow without any sign of agonistic behaviour and its actions were identical to those

when it followed its mother.

In the above interactions the male's behaviour was neutral in the sense that he neither encouraged nor prevented the joey from following him. The only times that a male exhibited aggression towards a young juvenile in the form of a chase or a fight was when more than two males were following an oestrous female, and there was a good deal of general excitement generated by interactions between the males and the female and between the males themselves. The earliest observation of such aggression occurred when Gus and Male 20 were closely following Hester who was accompanied by her 187 day old joey. Male 20 followed Hester up a small tree but immediately Gus also climbed the tree and chased him to the ground, where the chase continued. There was some confusion and at one point Male 20 attacked the joey and held it to the ground while it screeched. This immediately brought both Gus and Hester running towards them, and it was Gus who attacked Male 20 and chased him off the joey. Gus then spun round and chased Hester for two to three metres.

During the mating sequence involving Lesley, Donald and five other males, Lesley's 9 month old joey was twice chased by a male. The first time it was chased up a nearby small tree when it had been following its mother. It was still in the same small tree when a second male climbed into it and chased the juvenile higher. In neither case did the male attempt to catch the juvenile and in neither case was it the dominant male - Donald - who chased it. In fact Donald had trotted across the 18m from the tree that Lesley was in to chase the second male.

Gus' reaction to Male 20's attack on Hester's joey, and Donald's apparent reaction to the male chasing Lesley's joey, may have been a response to the aggressive behaviour of the other males irrespective of the fact that they were attacking juveniles. In the cage, I once removed the 4 month old joey from its mother and put it on the floor where it began to give distress zick-zick calls. The female (a very shy individual) did not respond to her joey's call, but the male in a separate nest box immediately became interested. He jumped to the floor and approached the

joey who by this time had climbed the side of the cage. He approached very cautiously and sniffed at the joey but I returned the joey to its mother when he appeared to be about to take a gentle bite at it.

5.72 Interactions with older juveniles

5.721 Male juveniles

From about eight months onwards interactions between adult males and juveniles change with noticeable differences depending on the sex of the juvenile.

Fewer observations were made of adult males interacting with juvenile males than with juvenile females (Fig. 5.35 b & c). This was partly because most observations were made on females having female joeys. However, the increased number of male-female juvenile interactions observed from 11 to 14 months was the result of young females becoming sexually attractive.

The adult male retains his dominance status throughout the period of interactions with a juvenile male, and only once was a young male observed to win an interaction (Fig. 5.35b). In it a 10 month old juvenile displaced a young adult male (Male 33, 32 months old) from a den in the maternal den tree at dawn. The juvenile's mother was in another den in the tree, and she had had an interaction with the adult male before entering their dens, which may have accounted for the juvenile being able to displace the older male.

All interactions with juvenile males up to the age of 13 months were of the give-way type (Table 5.43) and all were mild with no vocalisations at all, except for a short sharp grunt in one. In only one was there apparently any deliberate attempt on the part of the adult to supplant the juvenile. Jack sniffed the ground where Gerald (362 days old) had been, just before climbing a tree. Jack climbed the tree, chinning a branch as he climbed, and Gerald shot down the tree past Jack who took no apparent notice of him but continued to climb the tree. Nevertheless this appeared to be a clear case of supplanting, as all other give-way interactions merely involved the younger male withdrawing when they met.

Table 5.43

Type of adult male-juvenile interaction in relation to sex and age of juvenile. (⟶ = one interaction contains two types)

	♂ Juvenile			♀ Juvenile		
Interaction	Give-way	Chase	Fight	Give-way	Chase	Fight
Age - months						
5	-	-	-	2	-	-
6	-	-	-	5	-	-
7	1	-	-	-	-	1
8	-	-	-	1	-	-
9	-	-	-	3	2	1
10	2	-	-	1	1	1
11	4	-	-	11	1	-
12	1	-	-	16	3⟶2	
13	1	1⟶1		6	1	-
Total	9	1	1	45	8	5

More aggressive interactions were observed for the first time at 13 months. In one there was a subdued screech and I found Victor and young Gerald about 5m apart with Gerald looking towards Victor, obviously following an encounter. Victor then approached Gerald who stood and watched him until about 2m away, before breaking away and running to one side without Victor following. In another interaction involving Gerald 6 days later, Gus chased and caught up with him, biting at his hindquarters. One of them gave a grunting growl.

5.722 Female juveniles

One reason for the more frequent interactions between adult males and juvenile females was that males began to show a definite sexual interest in the young females older than 9 months. The two earliest estimated conceptions were 274 and 283 days i.e. 9 months. The change from a relatively neutral attitude of the male towards the juvenile female to that of definite interest was reflected in a number of trends. First there was an increase in interactions during the 11th and 12th months (Fig. 5.35c) mainly as the result of observations on two young females which apparently became sexually attractive at that age.

Secondly this increase coincides, although out of phase by one month, with most estimations of a young female's first conception (Fig. 5.35d). Thirdly there is a trend for more interactions to be accompanied by screeches with 11 and 12 month old juveniles (Fig. 5.35e). Screeches are typical of courtship type encounters between males and females as discussed earlier. Also in two interactions, with females 11 and 12 months old, the courtship shock-shook call of the male was heard.

Finally, the dominance status of the male in relation to the young female began to change to that seen between adult males and adult females. This is reflected in the trend shown of an increasing proportion of wins by a juvenile female which first becomes apparent at about 11 months (Fig. 5.35c), and in the increase in the number of interactions accompanied by a screech. This change in dominance in relation to the sex of the joey can be shown to be significantly different by the end of the 13 month (Table 5.44), and the change was observed to begin at the age of 8 months.

Table 5.44

Outcome of interactions between adult males and juveniles tested for independence on sex of juvenile. Interactions with juveniles 13 months and younger pooled.

		Sex of juvenile		
		Male	Female	Total
Male	wins	9	28	37
	losses	1	26	27
	Total	10	54	64

$G = 4.006$ 1 d.f. $p < .05$ + (Yates' correction used)

The earliest observation of a juvenile female winning an interaction was a low intensity one in which a 243 day old juvenile came down onto a feed trough and when about 0.6m from Donald (a high status male) the male turned aside and climbed to the ground. This was not a deliberate supplanting interaction by the young female, but she showed no signs

of nervousness towards the male.

The clearest example of the change in dominance at an early age was an interaction between Male 9 and the 304 day old Female 36 (joey of Female 6147). Both females came out of the same den and were soon joined by Male 9. About 4 min after Female 6147 had chased the male, the young female began to approach him. She came within 0.5m before stopping to sit staring intently at him. For the next 10 min, the young female gradually, centimetre by centimetre, moved closer. When within 0.3m of the male she several times turned her head away from the male, as though to reduce the tension between them. At first the male was sitting in a relaxed position taking little notice of the other. However, when she came within 0.3m he made a slight lunge towards her and there was a hiss but she did not move. Gradually she moved round Male 9 crabwise so that she continued to be pointing in his direction, until she was able to sit on the lower lip of the den entrance with the male on the upper lip about 15cm above her. Two or three times the male made an intention movement towards the young female. Each time there was a hiss, I think made by the female, and once she suddenly crouched and looked up at the male. Finally there was a short but definite fight, I think initiated by the juvenile, with several loud screeches and a grunt, and it was the male who broke away to hang head down, with his tail twitching, on the trunk about 1m away. The outstanding features of this interaction were the determined approach by the young female and her persistence in remaining close to the male. She, however, did not display the usual confidence of an adult female in such interactions, her lack of it being expressed by her head turning and the very slow approach. About 8 min later she dashed past the male in a give-way interaction when descending the tree, emphasising the transitional stage of their dominance relationships. Female 6147 had been sitting 3-4m above the two during the interaction and during the fight she began to come down towards them but stopped about 2m above them. Her presence may

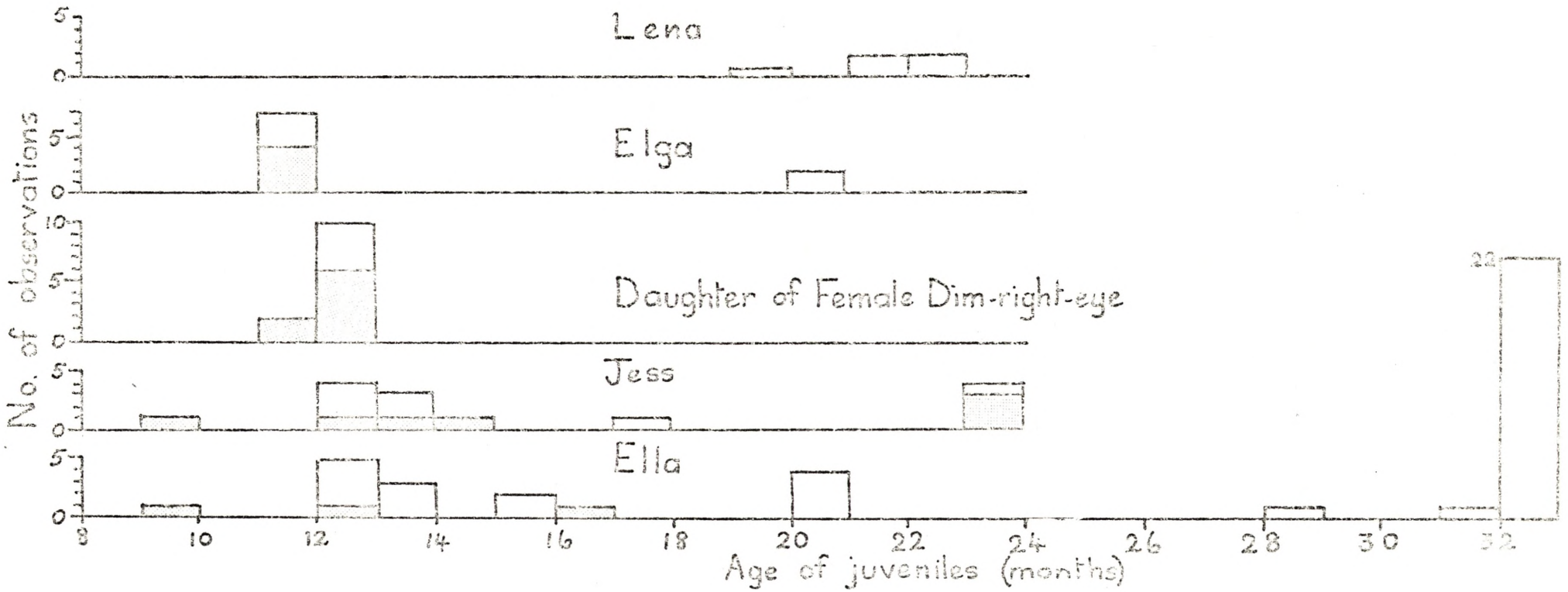


Figure 5.36 : Interactions between adult males and individual juvenile females in relation to age of female. Winner of interaction, shaded = adult male, blank = female.

have assisted her juvenile in winning the interaction.

There is a certain amount of individual difference as to when the young female becomes dominant to an adult male. In the case of Ella, for example, her behaviour at the age of 12 and 13 months towards an adult male was typical of an adult female. Not only did she win most of the interactions, but in two out of eight she chased the adult male (Fig. 5.36). Ella was one of the females recorded as having conceived at 9 months and this may have influenced her interactions. Two other young females (Elga and daughter of Female Dim-right-eye) on the other hand at 11 and 12 months 'lost' a high proportion of their interactions with a male (Fig. 5.36) and appeared to be nervous of the males.

When Victor was courting Female Dim-right-eye he had a series of interactions with the 11 to 12 month old daughter over a period of 45 dyas, whilst she still shared her mother's den. The two interactions at 11 months were typical give-ways in the vicinity of her mother. By the time she was 12 months old Victor had ceased courting Female Dim-right-eye and transferred his attentions to the daughter. On five separate nights Victor was seen to follow the young female rather than her mother and to approach her in the typical manner of a courting male, with much sniffing of branches, olfactory marking and shook-shook vocalisations. The young female was apparently very nervous of Victor which she manifested by watching him closely and by giving way rapidly when he came within 2m. As she gave way Victor continued to follow at a steady pace so that they did not develop into chases, but they tended to continue for a greater distance than in a typical adult give-way interaction. Twice such an interaction was observed to develop into a chase. In the second chase Victor caught the young female by the hind-quarters and she turned and fought him briefly, the fight being accompanied by screeches and grunts. It was Victor who broke away and in a further three interactions Victor was the possum that withdrew. Of the 10 interactions recorded during this courtship phase only 4 were accompanied by screeches, and in all 4 Victor withdrew. Thus, although the young

female appeared nervous of Victor and usually gave way to him, typical adult female reactions to an approaching male were beginning to develop. Elga, at 11 months, showed similar nervous behaviour towards Male 22 when he was courting her. In the three interactions which she won (Fig. 5.36), all were accompanied by screeches, but so did two of the interactions won by the male, once at the beginning of a chase, and once when the male lunged at her and she gave a screech as she hurriedly moved back. Nine months later Elga behaved as a typical adult female during two interactions with Male 33. When 19 to 23 months old Lena had five interactions with three different adult males. In all five she behaved as a typical adult female and won all the interactions (Fig. 5.36). On the other hand Jess, who had behaved as a juvenile female during her interactions at 12 to 13 months, was still apparently very nervous of Don, and lost most interactions (Fig. 5.36), when he mated with her when she was 23 months old. When he first climbed into the tree she shot higher up the tree. This was followed by a series of chases in which she appeared to be trying to escape from Donald. Only once, after mating, did she approach Donald, making a short run at him which caused him to turn and unhurriedly withdraw down the branch.

In general therefore an adult male becomes sexually interested in a juvenile female when she is eleven months old. At this time the young female is still nervous of the male although she is beginning to show signs of adult female behaviour. By 19 months however the female behaves as an adult, although there is a considerable variation, with some females behaving as an adult by 12 months, whereas others may still show signs of juvenile behaviour at 24 months.

5.73 Discussion

At Moggill Farm the male brush-tail possum played no part in the actual rearing of the young possum, and the few observations of male "protection" may have been incidental to aggressive encounters with other males. However, a male was demonstrated to respond to a joey lost call in a cage situation. Male common ring-tail possums (Pseudocheirus

peregrinus) who may share the nest with the female for extended periods, has been recorded carrying the young on his back (Marsh 1967). At low densities of brush-tail possums where den sharing is rare, there is little opportunity for this type of paternal behaviour. However, in the higher densities found in New Zealand and where den sharing is reported as a regular occurrence (Crawley 1973, Pracy and Kean 1969), this type of behaviour might occur.

Conversely the male shows little aggressive behaviour towards a juvenile younger than 8 to 9 months. His behaviour is predominantly neutral, but a mother will drive him away following a face to face interaction with her joey, suggesting that a male's behaviour may not be as neutral as it appears.

From about eight months onwards an adult male's behaviour towards a juvenile begins to show changes associated with the sex of the juvenile. He retains his dominance status over juvenile males, and at some stage begins to manifest more aggressive behaviour towards the young male, possibly when the latter is about 13 months old. With juvenile females, however, an adult male begins to be sexually attracted, in some cases as early as nine months old and there is an accompanying change in relative dominance status until by the age of 19 months most young females are behaving as typical adults.

The significance of this change in behaviour with respect to the sex of the joey, in relation to dispersion of the juveniles will be discussed in chapter 6.53.

5.8 JUVENILE-JUVENILE RELATIONSHIPS

No interactions between juveniles were observed when they were still following their mothers. In all of the interactions between adult females there were none in which both females had a joey out of the pouch. Very occasionally two adult females would come within the vicinity of each other but not have an interaction, and once or twice the females were accompanied by their joeys. One example of this occurred when Eve,

closely followed by her 211 day old joey, climbed into a tree already containing Jill with her 196 day old joey tucked under her. The two females were in the same tree for 1.75 hrs. Eve spent the time near the top of the tree feeding, with her joey also feeding at the same level and up to 4-5m from her. Jill spent the first 20 min on a low branch 5-6m below Eve, and her joey sat touching her. When Jill did move up the tree to feed in the canopy of the opposite side to Eve, Eve's joey moved rapidly across the tree to its mother while Jill's joey kept close to its mother the whole time. This observation would appear to be typical of joey behaviour when two females both with joeys are in the same vicinity. The joeys keep close to their respective mothers and take no interest in the other joey.

Only three interactions between juveniles were observed and in all three the juveniles were between the ages of 11 and 14 months. It consisted of two short chases on the ground interrupted by a pause during which they eyed each other. It was Ella, the younger of the two, who did the chasing in both cases and both chases were accompanied by short grunts and screeches. Twenty minutes later Ella chased Gerald, a juvenile male of 13 months, down a tree and continued the chase on the ground. On the ground the chase was again interrupted by a pause as they eyed each other. In both chases one of them gave a brief chatter. When Ella stopped at the end of the second chase Gerald kept travelling until he was well away from the young female. In the third interaction Gerald (12 months) and Jess (11 months) met on the bole of a tree with Gerald 2-3m above Jess. They remained in this position (both facing up the tree) for several minutes before Jess turned and jumped to the ground.

When Ella behaved aggressively in the first two interactions she already had a joey in the pouch which may have accounted for her relatively high level of aggression. The third interaction was a relatively neutral one between two young possums who appeared to have met accidentally.

Little can be said about juvenile-juvenile interactions except that there appears to be no evidence of amicable behaviour between juveniles, and there was no trace of social play between juveniles which is a feature of many mammals. In the group-living whiptail wallaby Kaufmann (1974) found play to be "....conspciuously inconspicuous.", and to be limited to juveniles with their mothers. Thus as Kaufmann (1974) remarks the lack of play behaviour may reflect a general marsupial characteristic.

5.9 FREQUENCY OF AGONISTIC INTERACTIONS

The frequency of adult agonistic interactions during the 1966 all-night observations was 0.207 per hr, with male-female interactions being the most frequent (Table 5.45). At times two possums would come close enough to each other for an interaction to take place, but instead the two drifted apart without apparently interacting. These are termed "non-action" interactions, and when included the total rate is 0.301 interactions per hr (Table 5.45). These figures are the overall rate, which varied considerably. During courtship the overall rate (over the 1968 courtship period) was 2.123 per hr (Table 5.46), and over shorter periods it was even higher than this. The highest rate recorded was during the multiple male mating sequence involving Lesley and six males (Ch. 5.21352) in which 4 give-ways, 19 chases, 6 fights and 7 mountings were recorded in a period of 1.5 hrs. This is a rate of 19.33 agonistic interactions (24.00 if mountings are included) per hr, and even this is probably a slight underestimate. The highest rate for an individual in this sequence was 16.0/hr (4 give-ways, 15 chases, 5 fights) for the dominant male, Donald. At the other extreme individuals went all night without an interaction with another possum. For example during the 1966 all-night observations only two agonistic interactions were recorded for 56.4 hrs of watching, a rate of 0.036/hr.

Table 5.45

Number of adult-adult agonistic interactions recorded during the 531.3 hrs of the 1966 all-night observations

	Non-action Interactions	Interactions	Total	Frequency/hr
Male-female	76	37	113	0.213
Male-male	21	6	27	0.051
Female-female	13	7	20	0.038
	110	50	160	
Frequency/hr	0.207	0.094	0.301	

Table 5.46

Number of adult-adult agonistic interactions recorded during the 57 hrs of Jan-Apr 1968 courtship observations

	Interaction	Frequency/hr
Male-female	88	1.544
Male-male	30	0.526
Female-female	3	0.053
	121	2.123

Agonistic interactions involving juveniles, but excluding mother-jcey ones, were even less frequent with rates varying from 0.004 to 0.015/hr depending on the age and sex of participants (Table 5.47).

Table 5.47

Number of adult-juvenile agonistic interactions recorded during the 531.3 hrs of the 1966 all-night observations.

	No. of interactions	Rate/hr
Adult male-juvenile male (16 months old)	8	.015
Adult male-juvenile female (12 months old)	5	.009
Adult female-juvenile male (excluding son)	2	.004
Adult female-juvenile female (excluding daughter)	3	.006
Juvenile-juvenile	2	.004

Frequencies of interactions given above appear to be low, and one is

tempted to attribute this to the fact that possums are solitary mammals. However, Grant (1973) records a rate of 0.022 decisive encounters per animal per hour for free ranging grey kangaroos (Macropus giganteus), which is considerably lower than the 0.207 per hr recorded in this study. Even allowing for possible differences in definition of agonistic interactions (his included only those which contained overt threat), and methods of collecting data (my figure was a total for all individuals, although no more than 3 or 4 would be under observation at any one time), the brush-tail possum frequency of agonistic interactions does not seem to be noticeably less, as one would expect in a solitary mammal.

Possibly more significant than the actual frequencies is the percentage of time spent in partaking of these interactions. For the brush-tail possum this was a low 2% for both males and females during the 1966 all-night observations, with a maximum time of 7.8% recorded one night for a consort pair (Ch. 3.62). In a less solitary species such as Macropus giganteus one can only assume, with the lack of data, that this time would be greater.

Chapter 6

DISPERSION

6.1 INTRODUCTION

In all four studies on the dispersion of the brush-tail possum (Dunnett, 1956, 1964, Winter 1963, and Crawley 1973) the pattern of dispersion is one in which the home ranges of the two sexes appear to be independent of each other, having an arrangement of male home ranges superimposed on a system of female home ranges without any evidence of discrete pair relationships.

Dunnett (1964) concluded from his two studies of possum dispersion in Canberra that "the evidence, both natural and experimental shows clearly that adult males are mutually exclusive and in general defend territories which are much larger than the undefended overlapping individual ranges of adult females". On the other hand, Crawley (1973) in his study on a New Zealand population at Crongorongo found that the ranges of neighbouring males overlapped considerably, territorial behaviour was not conspicuous, and that no part of a home range was reserved for the exclusive use of an individual. He gives two examples of males in which the individual range of one was shared by 11 other males, and in the other by 13 other males. Females behaved much the same. Clearly there appears to be a significant difference in the dispersion of males in the Canberra and Crongonrongo populations. Crawley attributed this to the different population densities at the two localities, being approximately 1.5/ha at Canberra and up to 10.6/ha at Orongorongo. In the lower population density at Canberra territories may develop whereas at higher densities a territorial system may break down. Batcheler et. al. (1967) have also suggested a break down of the territorial system of the brush-tail at densities in excess of 5 per acre, based on evidence from poison trials and removal trapping in New Zealand. Kean (in Batcheler et. al. 1967) maintains that it is above these densities that territorial behavioural mechanisms cease to function.

The evidence for or against territoriality of the brush-tail possum

has so far been inferred from the indirect method of trapping and has been based on the presence (Dunnett 1964) or absence (Crawley 1973) of exclusive areas as determined by trapping or on the pattern of captures in removal trapping (Batcheler et. al. 1967).

6.2. HOME RANGES AND MOVEMENT

Home range is the term used to denote the area within which an individual was usually observed (see Kaufmann 1962 and 1974 for general discussion of definitions). Dunnett (1956) has objected to the term home range being applied to an animal such as the brush-tail possum because they "....carry the young around, build no sort of nest, and use several shelters within the area of normal activity....". Instead he has proposed the term "individual range". However, I do not consider his objections warrant a change from the more generally accepted term home range, particularly in the light of observations in this study which show that females use only two dens on an average and that they will leave their joeys in the den at night while they feed away from the den tree.

One problem in any definition of home range is the "occasional sally" by individuals of some species of mammal, which Burt (1943) specifically excluded from his definition. However, it is not always possible to recognise the occasional sallies where only a few observations are made on an individual. Kaufmann (1962) has used the term "core area" for that part of a home range which is used more frequently than other parts, and the term "home range" to cover all movements, other than dispersal movements, of a group or an individual.

In the present study Kaufmann's (1962) definition of home range is used, except in the case of one male (Jack) where a distinction is made of one "occasional sally" well beyond his normal home range.

In the present study dispersion of the brush-tail possum has been determined by direct observation, and an attempt was made to relate the pattern of dispersion to behaviour.

The dispersion of the six central individuals studied during the

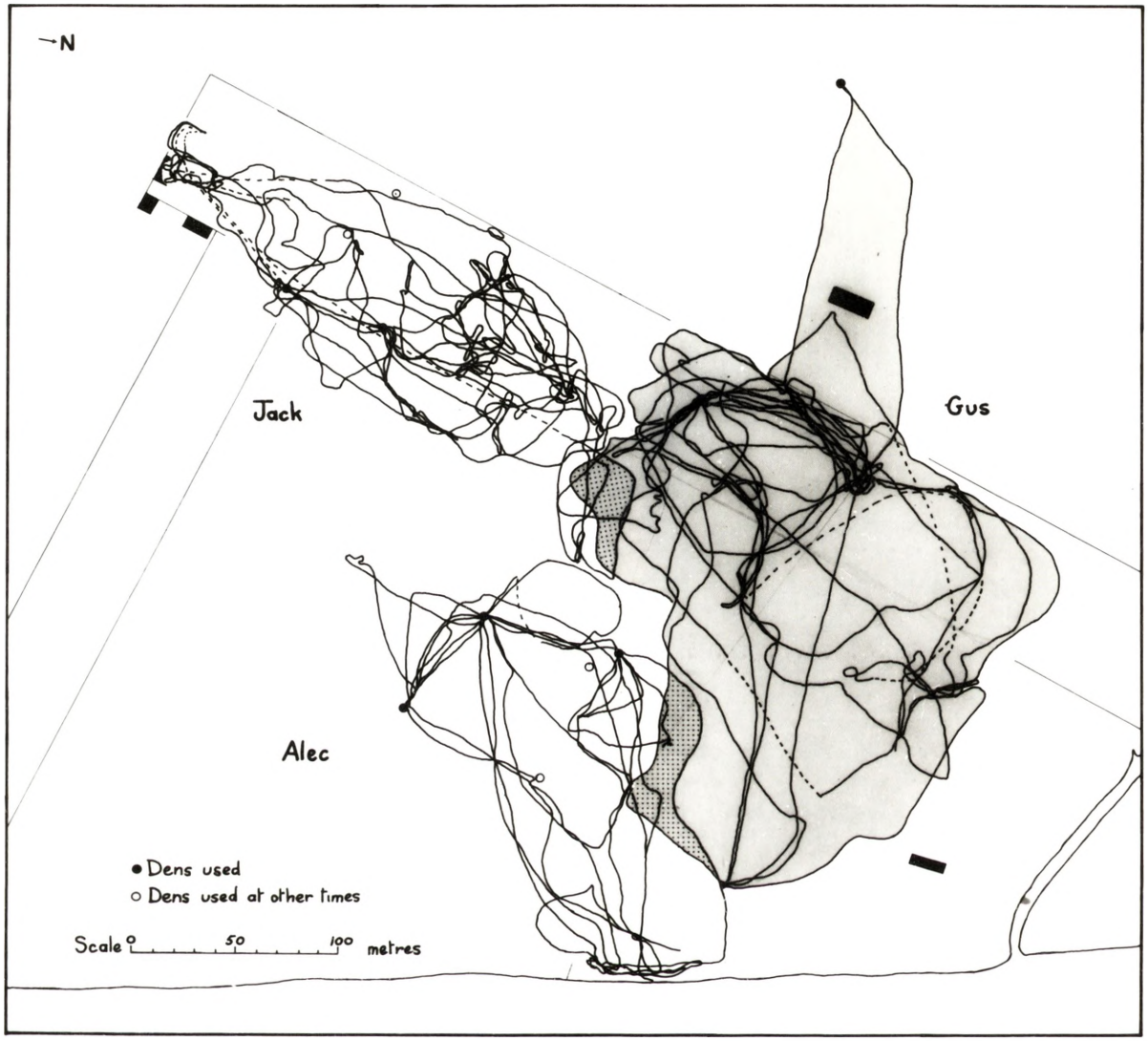


Figure 6.1 : Movements of the three central males when followed all night during 1966.
Continuous line = known movements;
dotted line = possible movements;
shaded area encompases Gus' movements;
stipple area = overlap between males.

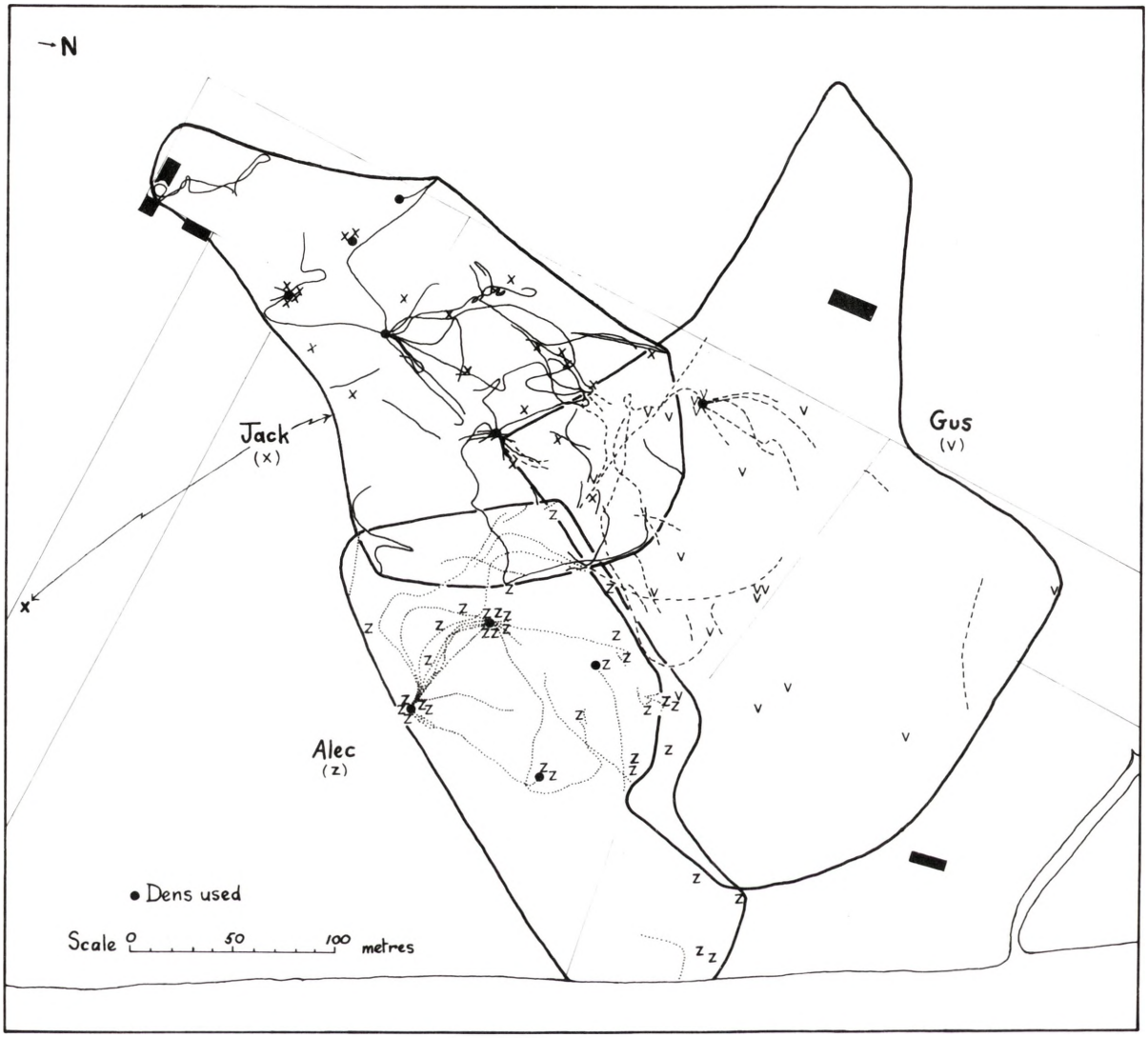


Figure 6.2 : Observations of the three central males in 1966 when not being followed all night. Letters = single observations; lines (continuous, dotted, and dashed) = movements; heavy line encompasses a male's home range based on all observations. Note one observation of Jack's is not enclosed within his home range (see text).

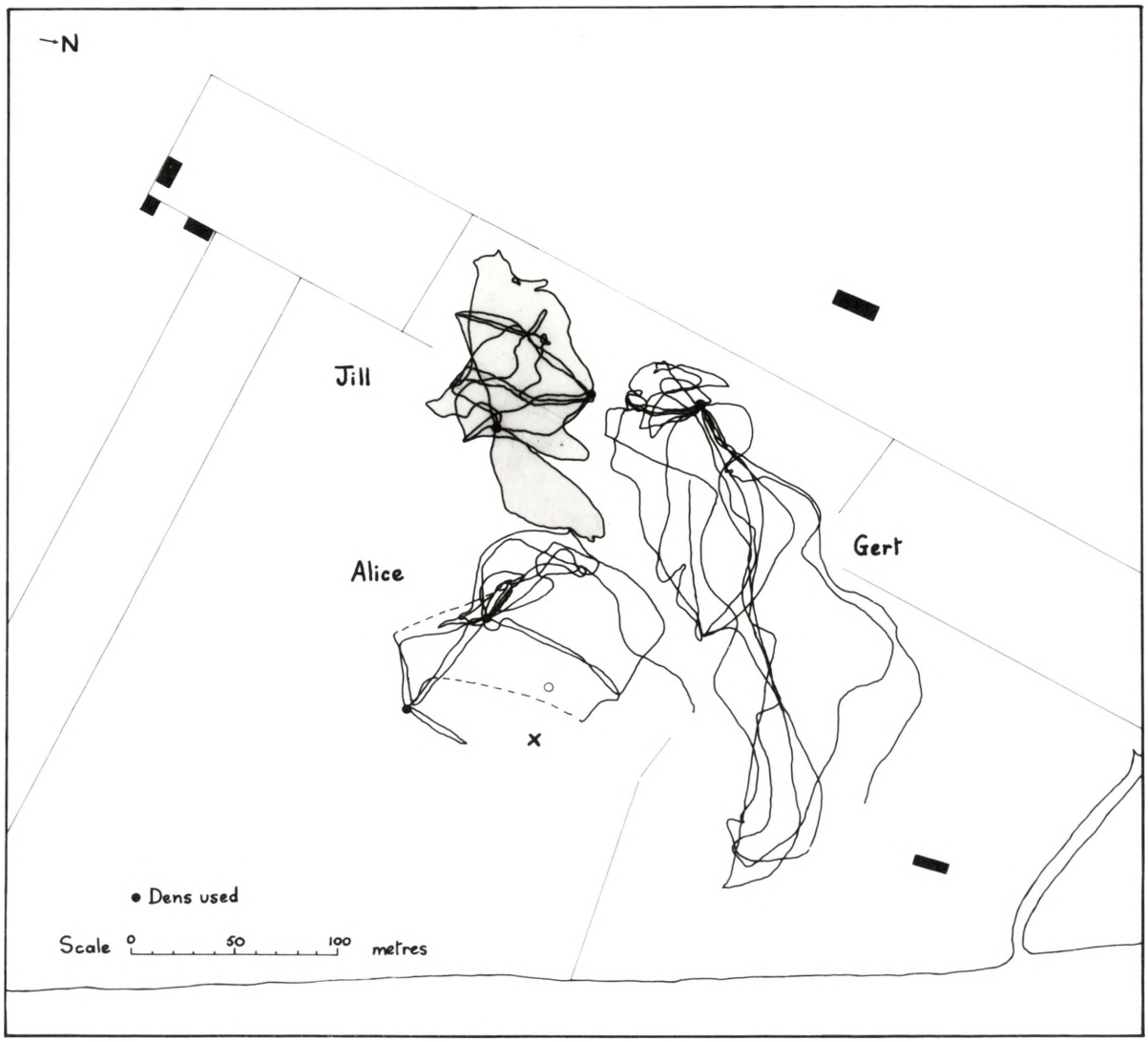


Figure 6.3 : Movements of the three central females when followed all night during 1966. Continuous line = known movements; dotted line = possible movements; shaded area encompasses Jill's movements. x = position taken up by observer at dusk when watching Alice.

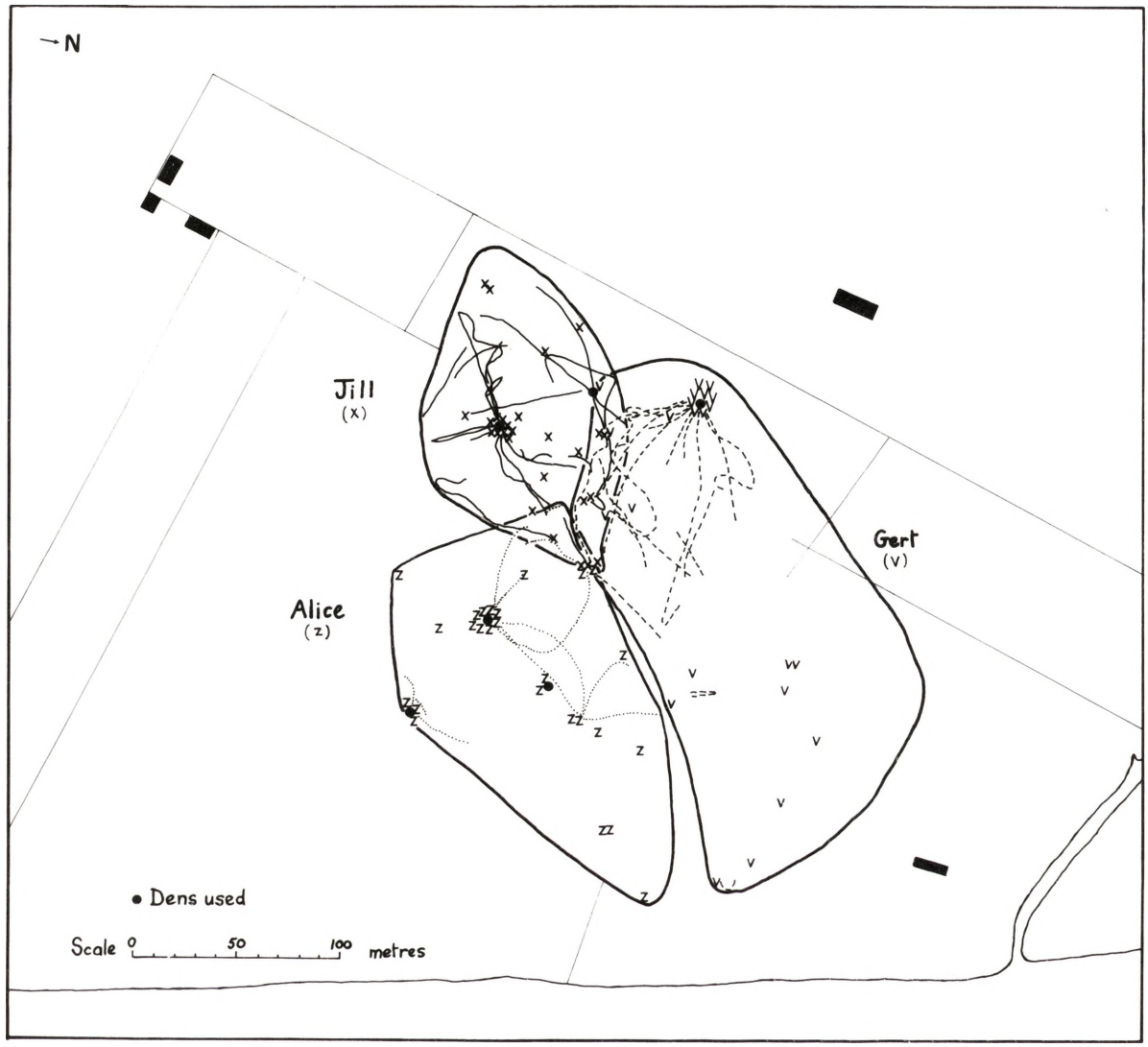


Figure 6.4 : Observations of the three central females in 1966 when not being followed all night. Letters = single observation; lines (continuous, dotted, dashed) = movements; heavy line encompasses a female's home range based on all observations.

all night observation period of 1966 is shown in Figures 6.1, 6.2, 6.3, and 6.4. They have been separated into male and female patterns as the Moggill farm population follows the general pattern of a male system of home ranges superimposed on a female system. The observations have also been separated into those obtained when following an individual throughout the night (Fig. 6.1 and 6.3) and observations obtained at other times, i.e. when another individual was being followed or during censuses (Fig. 6.2 and 6.4). Apart from presenting a less cluttered picture of the all-night movements, the separation in this way gives an indication of any undue disturbance caused by my constant following of an individual. In all individuals except Alice the difference between the all-night observations and the occasional observations can be attributed to factors other than my presence. For example, in the one observation of Jack well to the south east of where he was usually seen, he was seen with a group of three other males (Fig. 6.2). Presumably he and the other males had converged on a female in oestrus, (no female was actually seen on this particular occasion) and since such congregations of males occur for only one or two nights at the most, and only with a female who has lacked a consort male, the probability of such an observation is low. Gus' extension of home range to the north west in Figure 6.1 was across the strip of open ground to a den used by him only occasionally during the first 6-8 weeks of 1966. Since this den was just outside the study area he would only have been observed to use the den when he was the individual being followed. However, in at least one other observation (Fig. 6.2) he was seen to head in the direction of that den at dawn.

Alice was the only individual whose movements appear to have been curtailed by my watching her. In fact she was the shyest individual that I came across during the whole study. When I wished to follow her throughout the night I would take up my position at x (Fig. 6.3) which allowed me a clear view of the dens that she was known to use. Although I developed a technique for watching her, my presence at x apparently effectively restricted her movements to the north eastern end of her home range.

In the relatively open habitat of Moggill Farm there was no evidence of a track system developing on the ground. In the trees certain routes, particularly in the vicinity of den trees, were followed, and after a while it became relatively easy to predict the route to be taken. This lack of a track system on the ground is reflected in the relatively scattered configuration of routes followed as shown in Figures 6.1 and 6.3. There was some concentration of movements along corridors between focal points and particularly centered on den trees, but little more than that. This contrasts with the situation found in the forests of New Zealand where in areas of dense undergrowth very definite track systems may develop on the ground (Pracy and Kean 1969, Winter 1963, Crawley 1973).

Only in Jack's case was it possible to distinguish between a definite core area and one "sally" well beyond this area (Fig. 6.2). In the other five individuals no definite core area could be detected although with more intensive observations this may have been possible. Jack's movement beyond his core area is typical of movements by males converging on an oestrous female unaccompanied by a consort male. However, because such a congregation of males may last for only one or two nights, such movements could easily be missed. Many of the observations of peripheral males coming into the study area may be of this nature, as discussed later. In the following discussion the term home range embraces such movements, unless otherwise stated, because observations were usually insufficient to separate out occasional sallies.

Boundaries of the home ranges of the six central individuals are an arbitrary line encompassing the points of observation. The boundary was made concave at times and in the areas of contact of an individual's home range with that of another individual of the same sex, it followed very closely the peripheral observations (Fig. 6.2 and 6.4). Thus the area enclosed by this arbitrary line tended towards a minimum. In the case of Jack his one occasional sally to the south was not included within this home range boundary, because it lies well beyond the area usually used by him. Even if it was included, the method of drafting used would

Table 6.2

Observed range lengths of possums, 2 yrs and older, at Moggill Farm. Analysis of variance (Sokal and Rohlf 1969, Box 9.1) performed on individual years. Years not pooled because collection of data not strictly comparable from year to year (Ch. 2.22).

	1966		1967		1968	
	Female	Male	Female	Male	Female	Male
	267	399	237	418	205	315
	259	338	210	317	194	304
	222	299	205	299	185	
	219	293	196	297	180	274
	213	293	151	258	129	268
	198	289	141	256	127	239
	165	285	139	244	117	224
	141	276	127	161	94	217
	132	244	69	149	91	201
	129	211	55	146		140
		207		112		133
		159		104		
		152				
No.	10	13	10	12	9	10
Mean	194.5	265.0	153.0	230.1	146.9	231.5
SE	15.2	18.5	18.0	26.6	13.9	18.6
St.d.	48.1	66.7	57.0	92.2	41.7	58.9
F	7.2933		5.2999		12.7918	
d.f.	1,21		1,20		1,17	
p	<.025+		>.05 n.s.		<.005++	

show it merely as a thin finger-like projection. However, it was included in estimates of observed range length (Stickel 1954) which is the distance between the two observations furthest apart.

The male home ranges are larger than females' in area and the smallest male home range (2.7 ha) was larger than the largest female home range (2.6 ha) (Table 6.1). Although the difference in area was not statistically significant, observed range lengths of males (mean 337.67 ± 28.99m, n=3) were significantly ($p < .05^+$) longer than those of females (mean 207.33 ± 22.48m, n = 3) (Table 6.1), partly because Jack's occasional sally was included.

Table 6.1

Home range area and observed range length of the six central individuals, 1966.

	Males			Females	
	Area (ha)	Observed Range length (m)		Area (ha)	Observed Range length (m)
Jack	3.16[1]	338[2]	Jill	1.05	165
Gus	5.29	399	Gert	2.56	259
Alec	2.69	276	Alice	1.60	198
Mean	3.71	337.67		1.74	207.33
St. dev	1.131	50.215		0.624	38.939
S.E.	0.65	28.99		0.36	22.48

Male:Female area F=4.690; 1,4 d.f.; $p > .05$ n.s.

Male:Female observed range length F=8.414: 1,4 d.f.; $p < .05^+$

[1] Excludes the "occasional sally" (see text)

[2] Includes the "occasional sally"

Observations on other individuals and the six central individuals during subsequent years were insufficient to obtain a reasonable estimate of the area of the home ranges. Instead observed home range length is used for a comparison of the size of home ranges. Table 6.2 gives these values for the years 1966, 1967 and for the January-19th April 1968 period of observations. In all three periods the observed range length for males was greater than for females, but only significant for the 1966 and 1968 periods. The three periods are not strictly comparable because the data

Table 6.3

The distance travelled in one night by an individual possum when observed for the whole night during 1966. Analysis of variance (Snedecor and Cochran 1967, p227) performed on common logarithm transformation of data.

	Distance travelled (m)							
	Males				Females			
	Jack	Gus	Alec	Total	Jill	Gert	Alice	Total
	503	334	527		135	535	262	
	725	426	473		172	562	46	
	444	579	153		146	239	85	
	890	549	502		293	343	63	
	509	286	634		55	160	55	
	1630	665	556		252	786	272	
	465	579	316		178	175	279	
		728	573				193	
		955					144	
		312					193	
No.	7	10	8	25	7	7	10	24
Mean	738.0	541.3	466.8	572.5	125.9	400.0	159.2	234.3
St. dev.	394.2	199.6	147.2	279.29	72.4	217.4	88.7	173.04
S.E.	149.0	63.1	52.0	55.86	27.4	82.2	28.0	35.32
$\log_{10}$ transformation								
x	19.745	27.034	21.087		16.389	17.734	25.160	
Mean	2.821	2.703	2.636		2.341	2.534	2.516	
x^2	55.948	73.349	55.874		38.647	45.362	63.881	
Variance	0.036	0.027	0.036		0.039	0.062	0.058	
St. dev.	0.190	0.163	0.190		0.198	0.048	0.241	
S.E.	0.072	0.052	0.067		0.075	0.094	0.076	

Table 6.3 cont.

Analysis of variance on transformed data.

Source of variation	D.f.	S.S.	M.S.	
Individuals	5	1.027	0.205	F = 4.288
Residual	43	2.058	0.048	p .005 +++
Total	48	3.085		
Males	2	0.130	0.065	F = 1.764
Residual	22	0.809	0.037	p .10 n.s.
Total	24	0.938		
Females	2	0.165	0.083	F = 1.350
Residual	21	1.285	0.061	p .25 n.s.
Total	23	1.450		
Sexes	1	0.732	0.732	F = 14.611
Residual	47	2.353	0.050	p .001 +++

Table 6.4

Number of dens used by the six central individuals during 1966

	No. of dens		
	Males		Females
Jack	4	Jill	2
Gus	4+	Gert	3++
Alec	5	Alice	3

\+ 3 in tree Mt3
++ all in tree Mt3

Table 6.5

The number of individuals in relation to the total number of dens used by them throughout the entire study period

	No. of dens used							
	1	2	3	4	5	6	7	Total
Males	4	4	6	1	2	1	1	19
Females	11	10	4	2	2	1	0	30
Total	15	14	10	3	4	2	1	49

$G = 5.686$ 6 d.f. $p > .5$ n.s.

for the three years collected in different ways (Ch. 2.22). The most complete data were for 1966 with male observed range lengths (mean 265.0 ± 18.5m, n = 13) were significantly longer ($p < .025$) than those of females (mean 194.5 ± 15.2m, n = 10).

Males travel significantly further (mean distance 572.5 ± 55.9, n = 25) than females (mean distance 234.3 ± 35.3, n = 24) on any one night (Table 6.3 This indicates that the larger observed range lengths are a function of greater nightly activity rather than any seasonal shift in home range, although such a shift did occur in the case of Alec during the 1968 autumn breeding season (Ch. 5.214). The greatest distance covered by any one individual on any one night was 1630m (made by Jack) which the animal travelled by traversing the length of his home range approximately four times.

6.3 USE OF DENS

In the open eucalypt forest at Moggill Farm dens used by the brush-tailed possums were hollows in trees, and one or two in the ceilings of buildings. Unlike the ring-tail possum (Thomson & Owen 1964, Marsh 1967) the brush-tail possum does not construct a nest, and at Moggill Farm was restricted to the use of existing hollows in trees.

Dens therefore were important focal points in the home ranges. All those in regular use were at least 6m from the ground and had entrances no less than 10cm in diameter. A number of cavity openings existed close to the ground and there were a number of tree stumps (< 1m tall) with a hollow extending down the centre to below ground level. These low retreats were used only for emergency e.g. by a possum when released from a trap during the day.

During 1966 all six central individuals used from two to five (Table 6. Gert always used the same den tree, a large E.terreticornis, in which she used at least three of the four dens present, one more frequently than the others. Gus also used three of the dens in this tree. Trees with more than one den in them were not common in the study area and the use of different dens usually meant the use of different den trees.

Table 6.6

The number of consecutive observations of an individual possum using a particular den tree (multiple dens in one tree treated as one den). Sequences longer than 6 have been clumped as shown.

No. of consecutive observations	Males		Females	
1	62		57	
2	24		27	
3	9		12	
4	6		5	
5	1		8	
6	1		1	
7	1		2	
8	0	3	2	8
9	0		3	
10	1		0	
11			1	
12			3	
14			2	
15	1			
16			1	
17			1	
19		2	1	
20			1	14
22			1	
29			1	
31	1			
34			1	
50			1	
	107		131	

$G = 17.164$ 6d.f. $p < .01^{++}$

Table 6.7

Social use of dens at Moggill Farm, based on observations of the number of possums leaving a den at dusk.

	No. of Individuals involved	No. of Observations	%	
Adult female alone (± juvenile < 1 yr old)	26	477	60.9	89.5
Adult male alone	17	224	28.6	
Adult female + adult male	3 females, 4 males	23++	2.9	
Adult female + adult female	1 pr	3+	0.4	
Adult male + adult male	-	0	0.0	
Adult male + Juv male	1 pr	1	0.1	
Adult female + son > 1 year (< 16 months old)	1 pr	5	0.6	
Juvenile female (< 1 year) alone	7	31	4.0	
Juvenile male (using maternal home range) alone	3	19	2.4	
		783	99.9	

++ { Alice + Alec 8; Ella + Donald 1 } 9

{ Alice + Male 6214 (17-30 months) 13; Jess (13 months) + Jack 1 }

\+ All Alice + daughter Amy (12-13 months old)

There was a tendency for males to use more dens than females both in the observations given in Table 6.4 and for all observations on all individuals (Table 6.5). Although this tendency was not significant, when the number of consecutive observations of an individual using a particular den was compared there was a significant difference ($p < .01$) between males and females, with the females having longer sequences of observations for any one den (Table 6.6); females change dens less frequently than males.

Adults rarely shared a den on the same night (Table 6.7) as 89.5% of all observations were of solitary use of a den by either an adult male or an adult female with or without her joey. In 9 of the 23 observations in which adult males and females were seen to use the same den at the same time, both were well established individuals (Table 6.7), with the den sharing taking place during the consort period (Ch. 5.2113). In the other 14, 13 occurred when Male 6214 (between the ages of 17 and 30 months) shared a den with Alice. This den was at the northern extremity of his home range and at no time did he behave sexually towards Alice. Alice was probably his mother and he continued to use the maternal den while establishing a home range to the south. The one remaining observation occurred when Jack shared a den with the 13 month old Jess when she was in the process of establishing her home range. Thus the sharing of dens between well established adults of the opposite sex was less than 2% of the total observations. The three observations of two females sharing a den were all of Alice and her 12-13 month old daughter Amy, a case of a daughter continuing to share her mother's den. Within a month of this observation they had ceased to share a den. Apart from this last observation there were no records of adult individuals of the same sex sharing dens.

A measure of the exclusive use of a den by an individual is the number of individuals that use a den over a period of twelve months (Table 6.8). Over the three years from 38.1% to 55.6% of dens were used by only one adult possum during any of the 12 month periods (Table 6.8).

Table 6.9

Den usage over six month periods (see Table 6.8 for explanation)

	Number of dens											
	1966 Jan-June		1966 July-Dec		1967 Jan-June		1967 July-Dec		1968 Jan-April		1968 Sept-Jan (1969)	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1 Female	4	25.0	11	57.9	10	71.4	8	53.3	6	40.0	8	36.4
1 Male	4	25.0	1	5.3	2	14.3	3	20.0	4	26.7	3	13.6
1 Female+1 Male	4	25.0	2	10.5	2	14.3	2	13.3	4	26.7	8	36.4
1 Female + 2 Males	-	-	3	15.8	-	-	1	6.7	-	-	-	-
1 Male + 2 females	-	-	-	-	-	-	-	-	1	6.7	-	-
2 Females	3	18.7	1	5.3	-	-	1	6.7	-	-	2	9.1
2 Males	-	-	1	5.3	-	-	-	-	-	-	-	-
2 Females + 2 Males	1	6.3	-	-	-	-	-	-	-	-	-	-
3 Females + 1 Male	-	-	-	-	-	-	-	-	-	-	1	4.5
Total	16	100.0	19	100.1	14	100.0	15	100.0	15	100.1	22	100.0

Table 6.8

The number of possums using a den over a 12 month period. Den trees (two) containing more than one den, and dens peripheral to the study area are not included.

	Number of dens					
	1966		1967		1968	
	No.	%	No.	%	No.	%
1 Female	8	38.1	7	38.9	5	23.8
1 Male	1	4.8	3	16.7	3	14.3
1 Female + 1 Male	3	14.3	4	22.2	7	33.3
1 Female + 2 Males	2	9.5	1	5.6	1	4.8
1 Male + 2 Females	-	-	1	5.6	1	4.8
2 Females	3	14.3	2	11.1	2	9.5
2 Males	1	4.8	-	-	1	4.8
2 Females + 2 Males	3	14.3	-	-	-	-
3 Females + 1 Male	-	-	-	-	1	4.8
Total	21	100.1	18	100.1	21	100.1

The most common overlap of den use was with one adult male and one adult female with percentages ranging from 14.3 to 33.3% (Table 6.8), which is to be expected with the system of superimposed male-female home ranges. This means that from 57.1 to 77.8% of dens are used by only one individual of each sex. These percentages include permanent shifts in home range. To reduce this effect the time period was reduced to 6 months with a resulting increase in the exclusiveness of a den to one individual of each sex rising to 73.7 to 100.0% (Table 6.9). In 8 of the observations of two females using the same den during a six month period the two females were mother and daughter (the oldest daughter being 17 months), and only one observation was not of mother-daughter use. In this latter observation Jess (13 months old) once used Alice's den when going through an exploratory phase before establishing her own home range. The record of three females using a den involved the older female making a permanent shift to another den and the den continued to be used by her daughter and another young female. With dens used by two males in a six month period, three involved a well established male (Alec) and a young male (612A) who may have

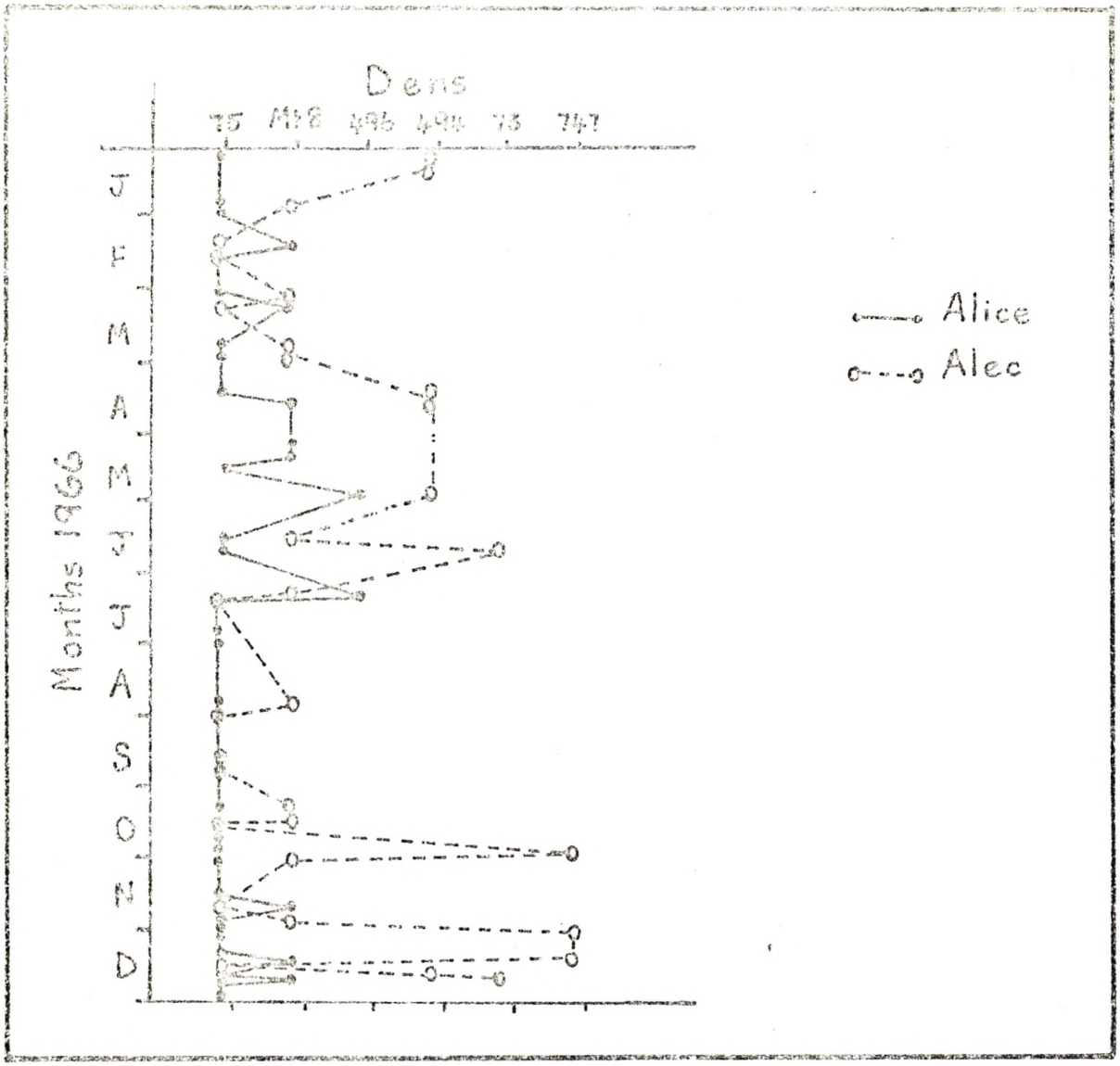


Figure 6.5 ; Use of dens by Alec and Alice during 1966.

continued to use his mother's den as he established a home range, and three involved well established males, two with Donald and Jack who had a clear dominance relationship (Ch. 5.33).

These records indicate a high degree of exclusive use of dens by individuals with respect to other individuals of the same sex, and the only significant overlapping of den use occurs between a male and a female.

Non-sexual interactions between the two sexes were centered on den trees and occurred more frequently at dawn when the possums were returning to their dens, and it was the females who won these interactions (Ch. 5.22). It follows therefore that adult females determined the use of a particular den each morning. Where there is an overlapping of the dens used by the resident adult male and adult female as in the example of Alice and Alec for 1966 given in Figure 6.5 this could mean that the male is frequently displaced by the female at dawn. However, the impression gained was that displacement was not usually caused by aggression. It was rather that males tended to wait until the females had returned to their dens before they themselves returned to their dens, and males did return to their dens significantly later than females (Chapter 3.61).

6.4 HOME RANGES RELATIVE TO STATUS OF INDIVIDUALS

6.41 Males

The home ranges of the three central males studied in 1966 barely overlapped with each other (Figure 6.2) thus suggesting that the home ranges in toto were synonymous with territories, (the exclusive area definition of territory (Pitelka 1959) is used), but when all observations on all males were examined the degree of overlap was considerable. This at first led me to believe that the situation observed for the three central males was anomalous.

However, it became apparent that there were two classes of males. First those that were in the process of establishing a home range/territory for themselves and, although adult, were subordinate males e.g. Male 22 and Male 32 and who acted as secondary consort males. Secondly those males

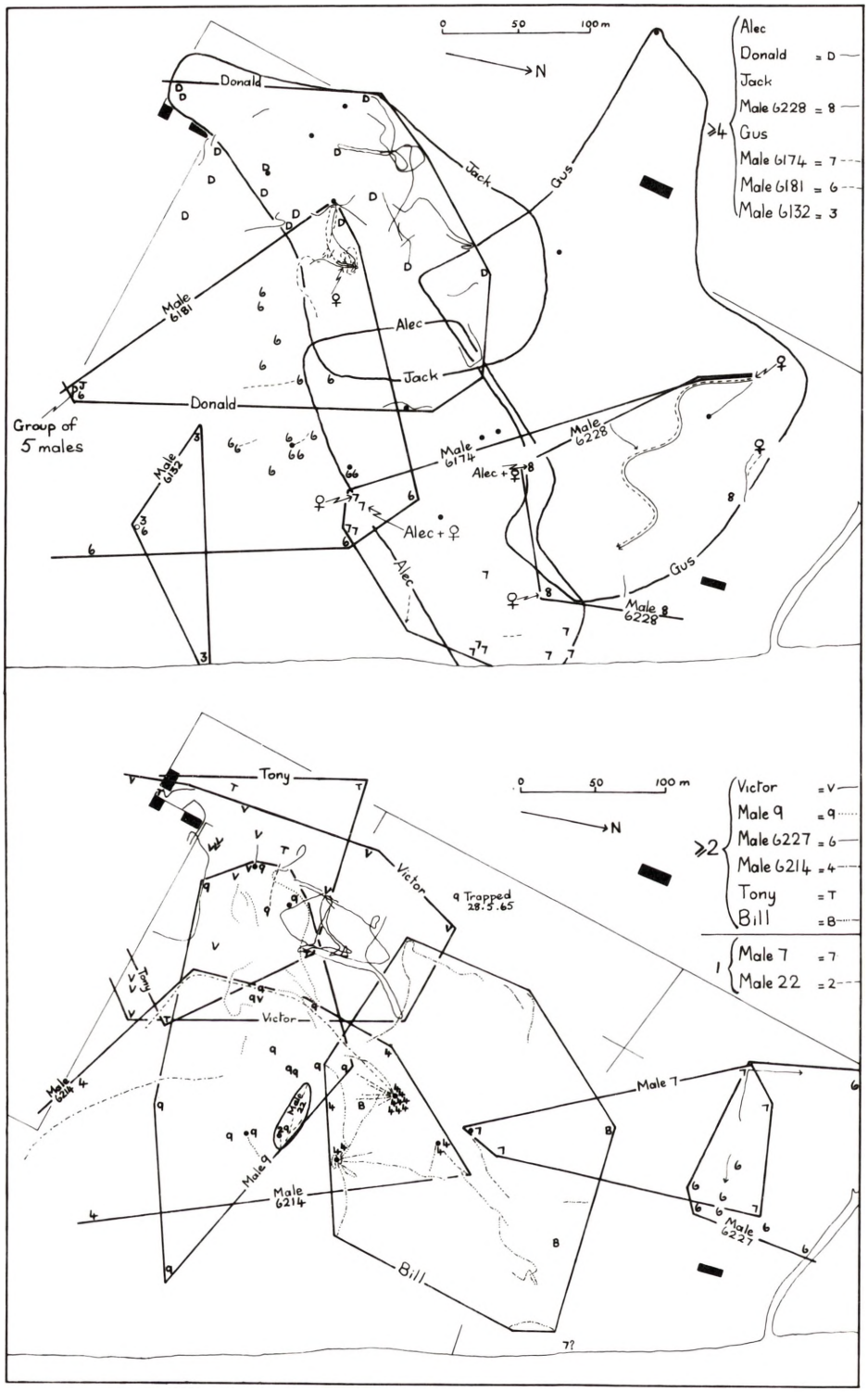


Figure 6.6 : Home ranges of all males for 1966. a) upper - 4 yrs old and over by the end of 1966. b) lower - males less than 4 yrs old (juveniles

that were older, well established males, e.g. Donald and Alec, who acted as primary consort males and were dominant to the younger males. Older males are dominant to younger males (Chapter 5.33) and with this age dominance stratification a definite pattern of male home ranges becomes apparent. Another important feature in the understanding of the overlap of male home ranges is the movements of males to join oestrous females, as exemplified by the occasional sally made by Jack.

Table 6.10

Age of male possums as at the end of 1966, 1967 and April 1968, of those individuals discussed in Figures 6.6, 6.7, and 6.8. +Age at time of disappearence before end of period.

	Age (yrs/months)		
Individuals	1966	1967	April 1968
Alec	7/10	8/10	9/2
Donald	6/5	7/5	7/9
Jack	6/2	7/1+	-
6228	5/5	6/5	6/9
Gus	5/4	6/0+	-
6174	5or6	-	-
6181	4	5	-
6132	3/7	4/7	4/11
Victor	3/2	4/2	4/6
9	3/2	4/2	4/6
6235	-	-	4
6227	2/6	3/3+	-
6214	2/6	-	-
Tony	2/2+	-	-
Bill	1/11+	-	-
7	1/10	2/10	3/2
22	1/8	2/8	3/0
16		1/6approx.	-
Jim		1/2	1/6
33			2/0
32			1/10

Figure 6.6a sets out the 1966 home ranges of males 4 yrs and over by the end 1966 (Table 6.10), and Figure 6.6b the home ranges for younger males excluding those which were still based on their mothers home range, because as shown later young males go through a definite dispersal phase out of the maternal area.

The overlap of the older well established males still appears to be considerable, but on closer examination most of this overlap is the result

of males converging on an oestrous female. For example the overlap in the home ranges of Donald and Male 6181 was almost entirely the result of two such sallies, one by each male. Male 6181's north western extension of his home range occurred during the mating sequence in which Donald prevented several males mating with Lesley, and Donald's south eastern extension was the result of an observation of a male congregation, presumably at a female (Fig. 6.6). Male 6174's southern extension of his home range with a resulting overlapping of Alec's home range, was the result of four observations and in two he was seen with Alice or in the vicinity of the consort pair Alec and Alice. Similarly in his two most north westerly observations he was in the vicinity of an oestrous female. Thus his core area was probably down by the river with a narrow zone of overlap with Alec in the tall E.terretecornis trees along the river bank. In the long chase following a fight over a female, Male 6174 headed for the river bank area, possibly his core area, closely followed by Male 6228. An unknown male with a distinctive white tip to his tail was twice seen in the study area. First when with Gert, just to the north of the overlap zone between the home ranges of Gus, Alec and Jack (Fig. 6.6a), and again three nights later during the mating sequence with Donald, Lesley and several other males. Each time he finally disappeared to the south west presumably to his core area which lay outside the study area.

One exception to this general pattern did exist. It was the almost total overlap of Jack's home range by Donald's. Both were six year old males by the end of 1966 and therefore considered to be well established males. There was however a clear dominance relationship between the two males with Donald being the dominant individual (Chapter 5.33). Donald was seen to mate with Lesley, Alice and Jess and to act as a consort male to Jill, all being females whose home ranges were almost totally encompassed by Jack's home range. Donald was once seen to climb a tree containing Jill and Jack and to chase Jack from the tree. Another time Jack followed Donald and Jill to the base of a tree which they climbed, but he remained at the base for about 5 min then moved away. Neither of these actions were

consistant with a primary-secondary consort male relationship but suggested a more aggressive dominance relationship.

The dispersion of males who had not reached 4 years of age by the end of 1966 (Fig. 6.6b), appears to be independent of the older males. Victor and Male 9 were the oldest (Table 6.10) of this group and their home ranges closely approximated those of Donald and Male 6181 respectively. During the mating sequence with Lesley, Victor was one of the more persistent males and the only one apart from Donald to start pelvic thrusting.

Males 6227, Tony, and 6214 were between two and three years old, and only Male 6227 remained in the study area during subsequent years. Tony disappeared at the end of June at the age of 26 months and Male 6214 in December at 30 months. Male 6214 regularly shared a den with Alice (his mother?) and was apparently establishing a home range just to the south east of the study area.

Bill was a younger male who disappeared in March at an age of 22-23 months. His home range closely approximated that of Alec's. In the 2-3 months before he disappeared he and Alec had several agonistic interactions. Once Alec chased Bill out of a den at dawn, another time he chased Bill from a tree which also contained Alice and her young son, a third time Alec chased him in a series of short ground chases when both were following Alice, and in a fourth interaction Bill left a tree after a 'deliberate' approach by Alec. Bill was probably not Alice's son because the earliest observations of him were to the north of Alice's home range. He was probably a young male in the process of trying to establish a home range, and Alec's antagonism possibly contributed to his disappearance.

Male 7 was observed for the first time in May when only 15 months old, and Male 22, who had a distinctive scruffy tail, did not appear in the area until December at the age of 20 months.

In subsequent years the pattern was much the same. Males estimated to be 4 years and older by the end of 1967 (Table 6.10) were relatively evenly spaced through the area with the same general pattern of a core

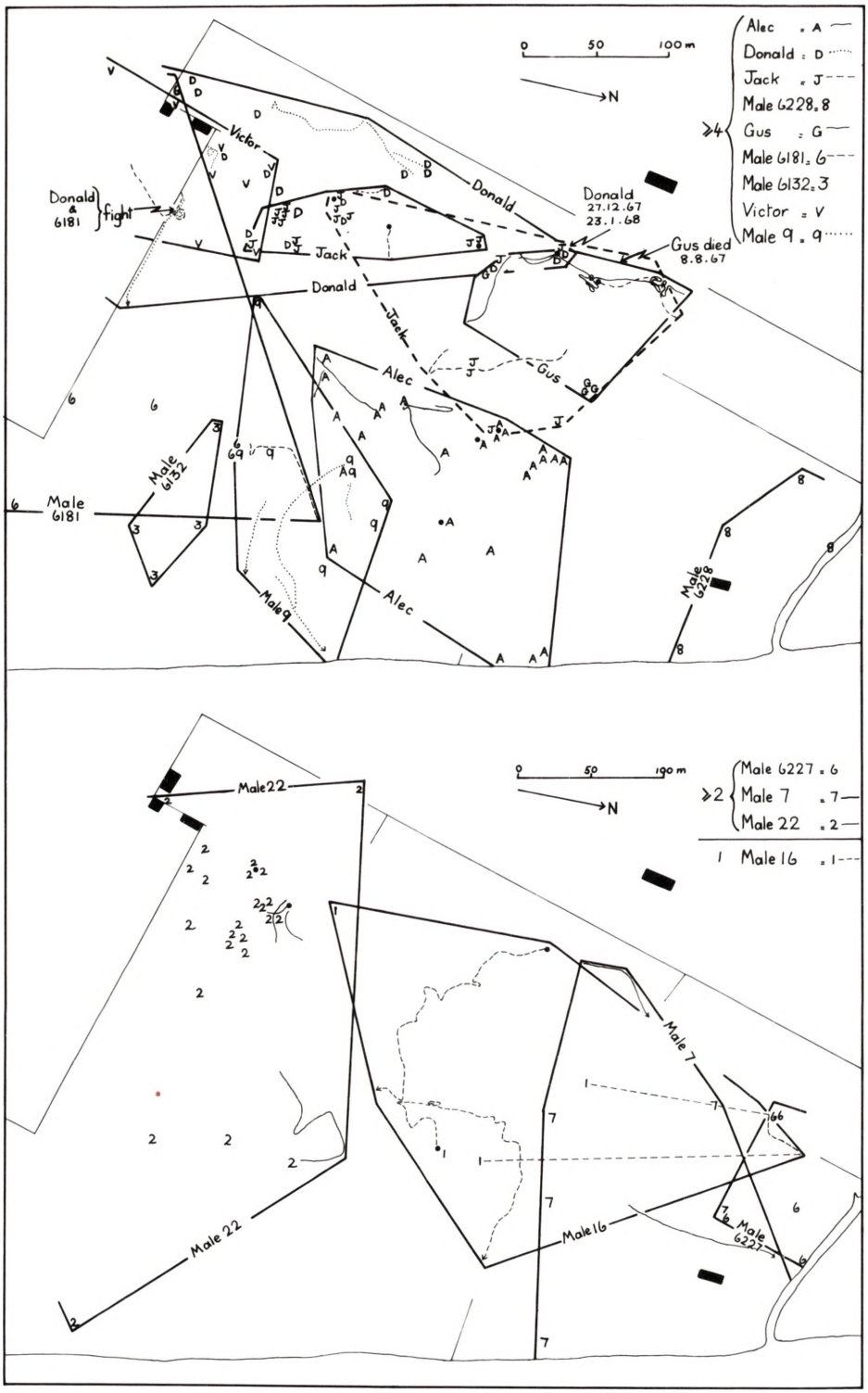


Figure 6.7 : Home ranges of all males for 1967. a) upper - 4 yrs old and over by the end of 1967. b) lower - males less than 4 yrs old (juveniles

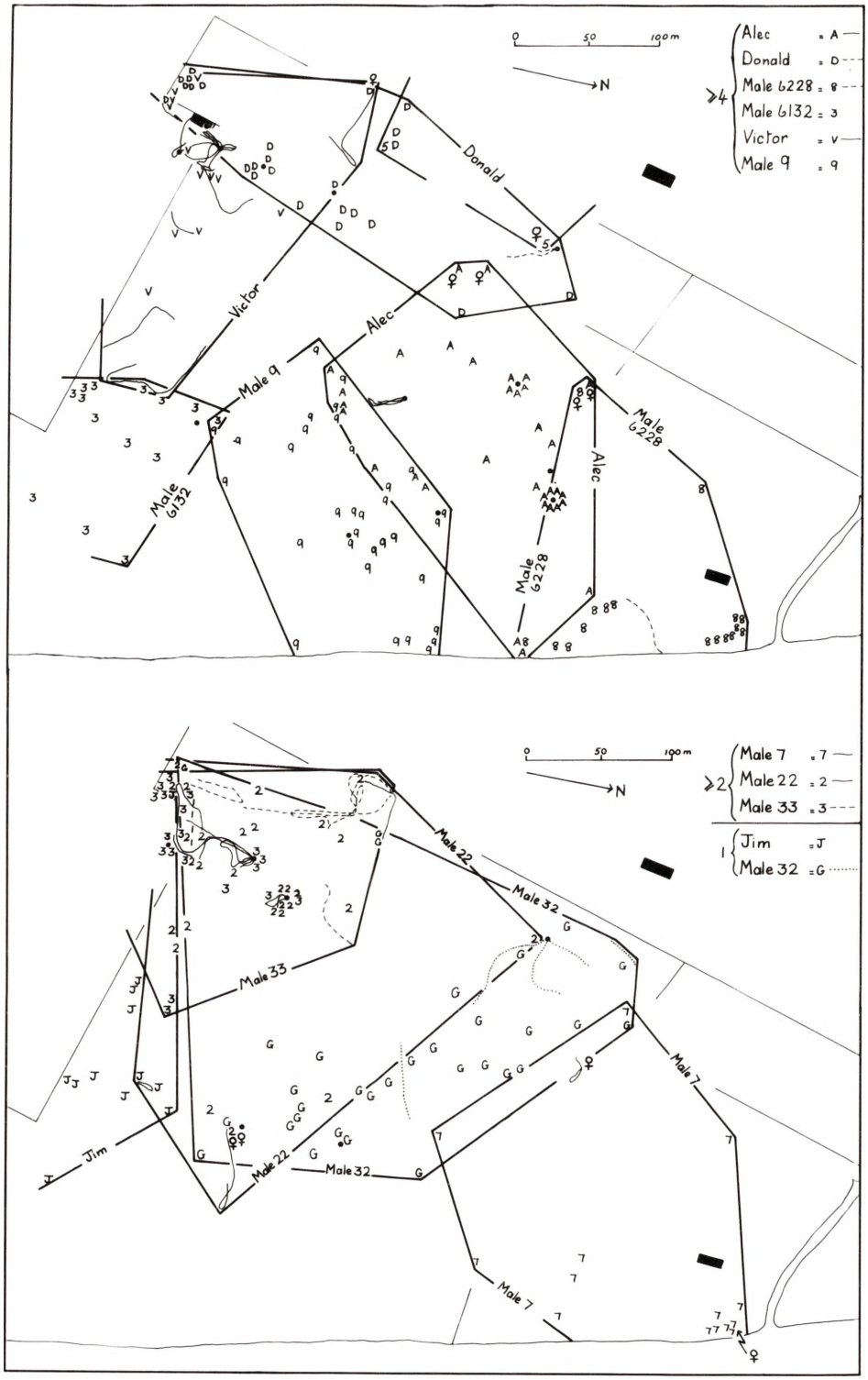


Figure 6.8 : Home ranges of all males for Jan - April (inclusive), 1968. a) upper - 4 yrs old and over by the end of April 1968.
b) lower - males less than 4 yrs old

area which tended to be exclusive (Fig. 6.7a). Observations on Gus were only made for part of the year as he was accidentally killed on 8th August. Very soon afterwards Jack made a major shift in his home range until by the end of the year his activities were centred on Gus' old home range. Male 6181 was in much the same area as in 1966. He and Donald had the long fight on the fence (Fig. 6.7a) which was the only fight seen between adult males away from the vicinity of an adult female and may have represented a territorial encounter. Males 9 and Victor had by now entered the "established" male category with Male 9 making an easterly shift to centre his activities towards the river by the end of the year. Donald's home range completely overlapped the observed home range of Victor but both used the area to the south of the study area where they may have had exclusive areas.

The dispersion of younger males during 1967 is shown in Figure 6.7b. Male 22 expanded his home range and towards the end was using dens in the western half of his home range which overlapped that of at least 3 older males, Donald, Victor and Male 6181. Male 7's home range occupied a gap in the home ranges of the older males left by the disappearence of Male 6174 during January. Male 16's appearence in August at the age of approximately 18 months coincided with the death of Gus and in fact Male 16 was observed using Gus' den on 9th September. However, it was Jack who eventually filled the vacancy left by Gus and Male 16 was last seen in the area on the 3rd October after he had shifted to a den in Alec's home range. It is inferred from the above observations that Male 16 was prevented from taking over Gus' den and home range by the older Jack.

Figures 6.8a and 6.8b show the home ranges of males during 1968 but only up to April 19th i.e. over the time of the main autumn breeding season. Compared with the observed home ranges over a period of a full year the overlap between the males, who were 4 years and older by the end of April, is very much less. This is attributed to the general lack of males converging on oestrous females, because this type of male behaviour tended to occur when a female was not accompanied by a consort male, and during

the autumn breeding season most females were accompanied by consort males. One exception was Eve who mated with four males. Two of these were Donald and Victor, and the observation of Victor with Eve in the north western part of his home range accounted for the overlapping home ranges of the two males. During February-March both Victor and Donald established consort relationships with Female Dim-right-eye and Ella respectively whose den trees were no more than 30m apart. Despite the proximity of the two males when with the females in the early part of the evening virtually no overlap occurred. Male 6235 was seen in the vicinity of Eve when she mated but he did not actually approach her, and 11 days later he was seen in the vicinity of Male 32 and Gwen. His home range was almost certainly to the west across the strip of open grassland and both these observations represent excursions to visit oestrous females. Jack disappeared in November 1967 and Donald was then the only older male in the area. Male 6228 appeared to have moved into the area vacated by Male 6174 early in 1967, while Alec, Male 9, and Male 6132 occupied virtually the same areas as in 1967.

Home ranges of males younger than 4 yrs by the end of April are shown in Figure 6.8b. The relationship of Male 32 and Male 22 to older males in their areas, notably Alec and Donald have already been discussed (Chapter 5.2124). They both acted as secondary consort males and were significantly more active than the older males. Male 33 was a newcomer to the study area possibly from the south. Jim was a young male establishing himself after leaving his mother's (Jill) home range. Male 7 was not often seen but he had not apparently shifted his home range despite the possible shift by Male 6228.

The above observations on male home ranges can be summarised as follows.

The home ranges can be separated into those of males who have reached the age of at least 4 years, and those of younger males, excluding the juvenile males who still centre their activities on the maternal home range. The older group of males appear to have <u>established</u> their home

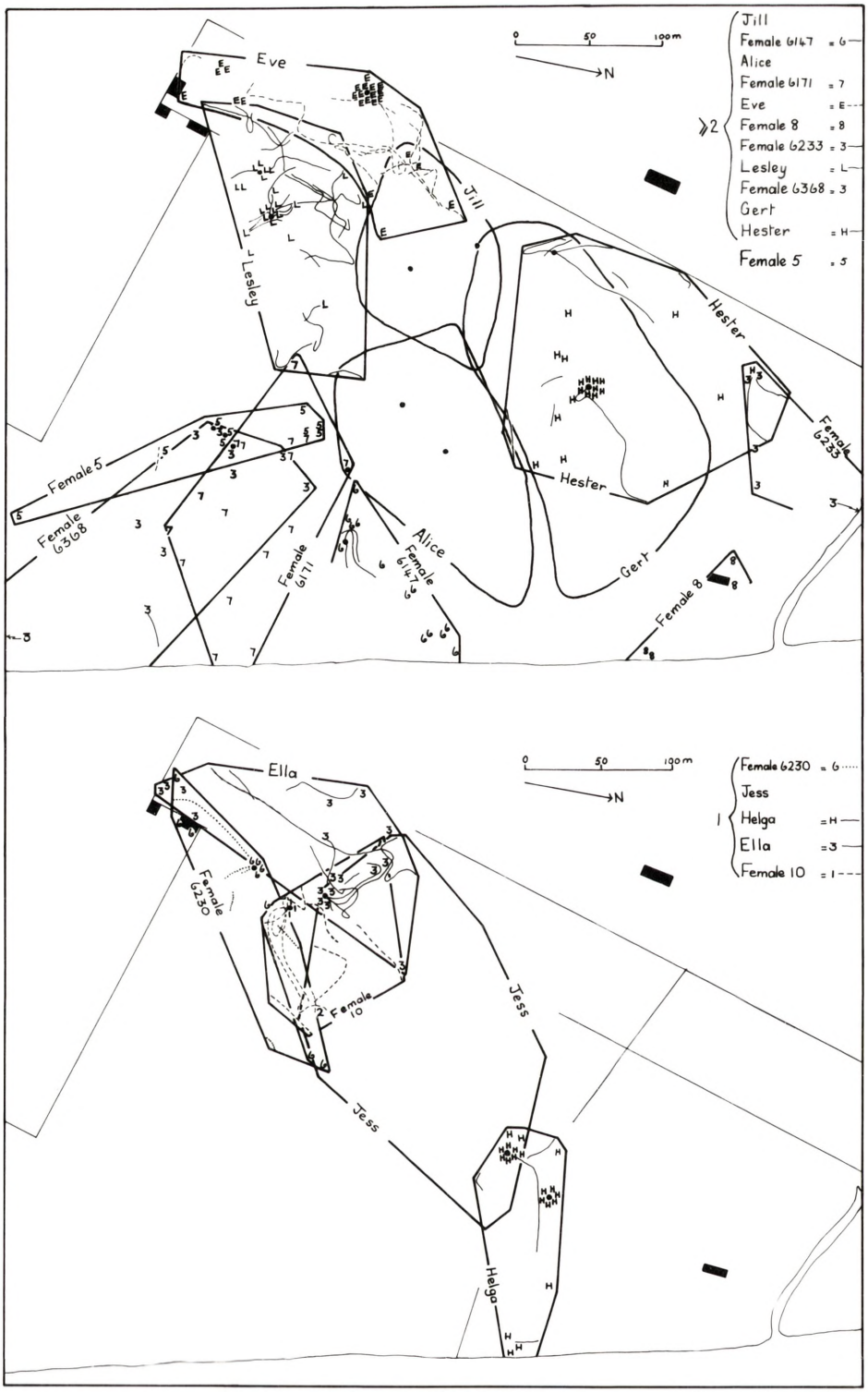


Figure 6.9 : Home ranges of all females for 1966.
a) upper - 3 yrs old and over by the end of 1966 (includes Gert and Hester who were 2 yrs 10 months and 2 yrs 9 months respectively).
b) lower - females less than in (a) but more than 1 yr old.

Table 6.11

Age of female possums as at the end of 1966, 1967 and April 1968, of those individuals considered in Figures 6.9, 6.10 and 6.11. +Age at time of disappearence before end of period.

Individuals	Age (yrs/mnths) 1966	1967	April 1968
Jill	6/3	7/3	7/7
6147	5/11	6/11	7/3
Alice	4/11	5/11	6/3
6171	3/9	4/9	5/1
Eve	3/8	4/8	5/0
8	3/2	4/2	4/6
6233	3/?+	-	-
Lesley	3/?	3/?+	-
6368	3/?	4/?	4/?
Gert	2/10	3/9+	-
Hester	2/9	3/9+	-
6230	1/8+	-	-
Jess	1/9	2/5+	-
Helga	1/8	2/8	2/11+
Ella	1/6	2/6	3/0
10	1/2+	-	-
Slit-ear	0/9	1/9	2/1
Moon-ear		1/6	1/10
Lena		1/6	1/10
White-tip		1/4	1/8
Hebe		1/3	1/7
Gwen		1/3	1/7
Dim-right-eye		1/2	1/6
Emily		0/8	1/0
Amy		0/8	1/0
Elga		0/8	1/0

5 25-44 months

ranges and once having done this there are only minor changes in the home range except in the case of Jack. The home ranges of these established males consist of a core area with relatively little overlap with core areas of neighbouring established males, and from this core area the male will make occasional sallies, often deep into a neighbouring established male's area to visit oestrous females, particularly those that have not been accompanied by a consort male. Younger males have home ranges which may completely overlap those of older males but with a tendency not to overlap extensively with each other. These younger males are in the process of establishing themselves and may shift their centre of activities as they settle into the area. Some of the establishing males are apparently not successful and disappear. The ability of a young male to maintain a home range overlapping that of an established male and eventually to establish himself may depend on being able to find a den not used by either a female or an established male. Establishing males act as secondary consort males and may even be able to act as the primary consort male if there is an excess of females but only if the established male apparently takes no interest in the female.

6.42 Females

Females also show an age-structured pattern of home ranges. For example the home ranges of the females for 1966 fall into two reasonably well defined categories. One group of females, all of whom were 33 months or older by the end of 1966 (Table 6.11), have a pattern of relatively little overlap of their home ranges (Fig. 6.9a). The exceptions to this were Gert and Hester, the two youngest females in this group (the home ranges of the females at the south eastern end of the study area were not well documented). As with the males the overlapping of home ranges was often mainly a function of the draughting technique, rather than a real overlap. For example, Eve's movements from her den were either southwards to the sheds, or to the east in a cresent to the west of Lesley's home range. Observations of actual overlap of these two females are minimal and this has been expressed by drawing a concave south eastern boundary to

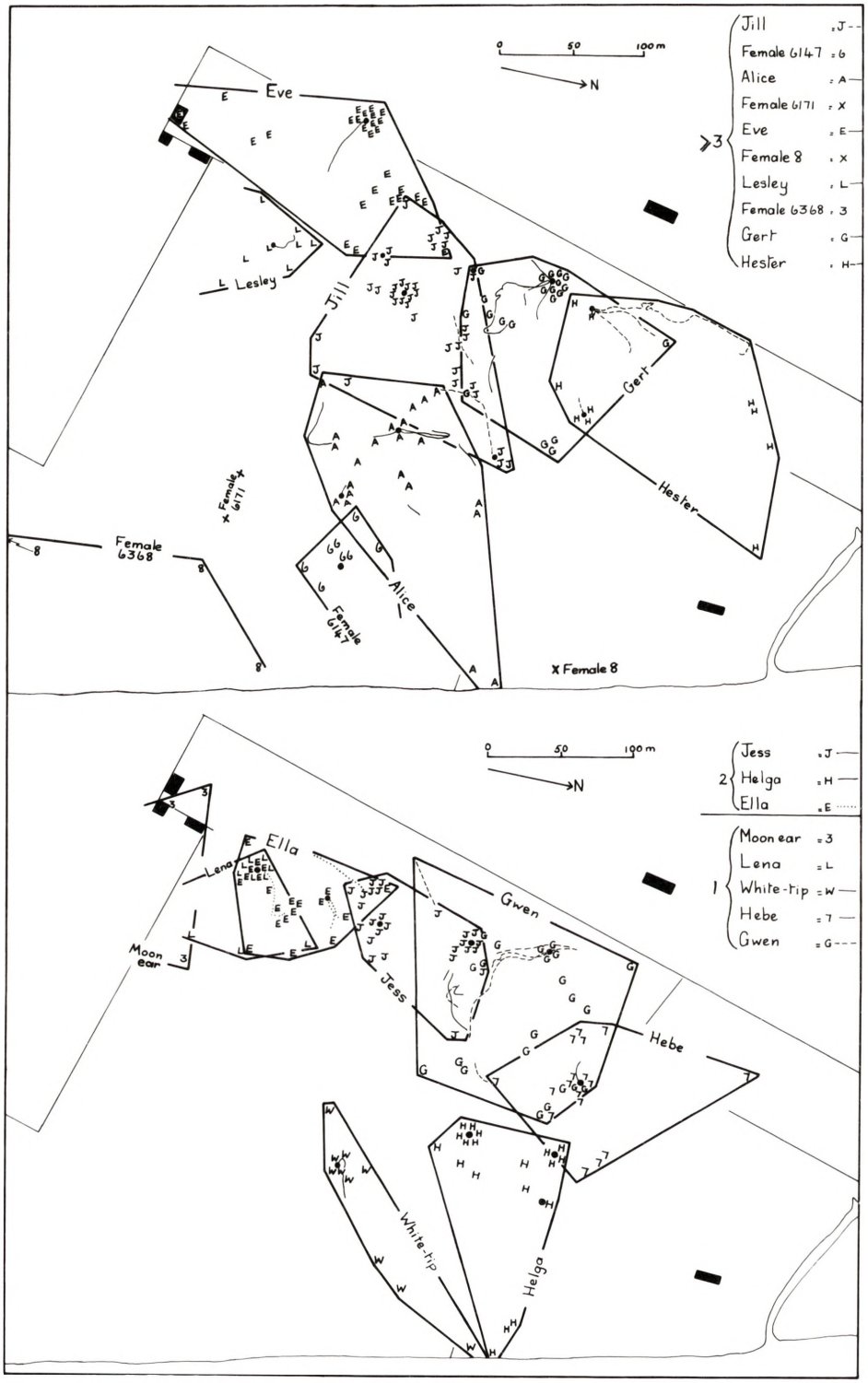


Figure 6.10 : Home ranges of all females for 1967. a) upper - 3 yrs old and over by the end of 1967. b) lower - less than

Eve's home range. The females of this older age group have extensive exclusive areas relative to one another and dens tend to be in these exclusive areas.

A younger group of females also occurred, none of them having reached the age of 24 months by the end of 1966 (Table 6.11), and their home ranges are shown in Figure 6.9b. It is obvious that their home ranges extensively overlap those of the older females except that of Helga who occupied a vacant area to the east of Alice's home range. Jess, Ella, Female 10, and Helga were the daughters of Jill, Eve, Lesley, and Hester respectively (mother of Female 6230 not known). All were in the process of establishing home ranges.

During 1967 there was little overlap of home ranges of females who were 3 years or older by the end of 1967 (Figure 6.10a). The overlap between the home ranges of Gert and Hester was less than in 1966, despite the shift of Hester's den to a tree 35m from Gert's. In fact the overlap was virtually nil because the observation of Gert in the northern corner of her home range was made in late November after Hester had been seen for the last time early in November. This may have represented an expansion of Gert into the area left vacant by Hester's disappearence.

Three younger females Helga (2 years 8 months), Jess (2 years 7 months) and Ella (2 years 6 months) represented a younger age class (i.e. 3rd year). Helga had apparently succeeded in establishing her home range among those of Alice, Gert and Hester (Fig. 6.10b). Ella expanded into the area left vacant by Lesley when she disappeared in April. Jess' home range was still totally overlapped by that of her mother (Jill), but they had settled down to the exclusive use of two major dens in the area. Also Jess had become dominant to her mother. Female 10, a member of this age class in 1966, had disappeared at the end of November 1966.

Figure 6.10b also shows the home ranges of females in the second year age class. Four (Lena, Hebe, White-tip, and Gwen) were daughters of resident females (Lesley, Hester, 6147 and Gert respectively) and their home ranges overlapped those of their mothers considerably except in the case of Female White-tip (this could be a result of inadequate observations).

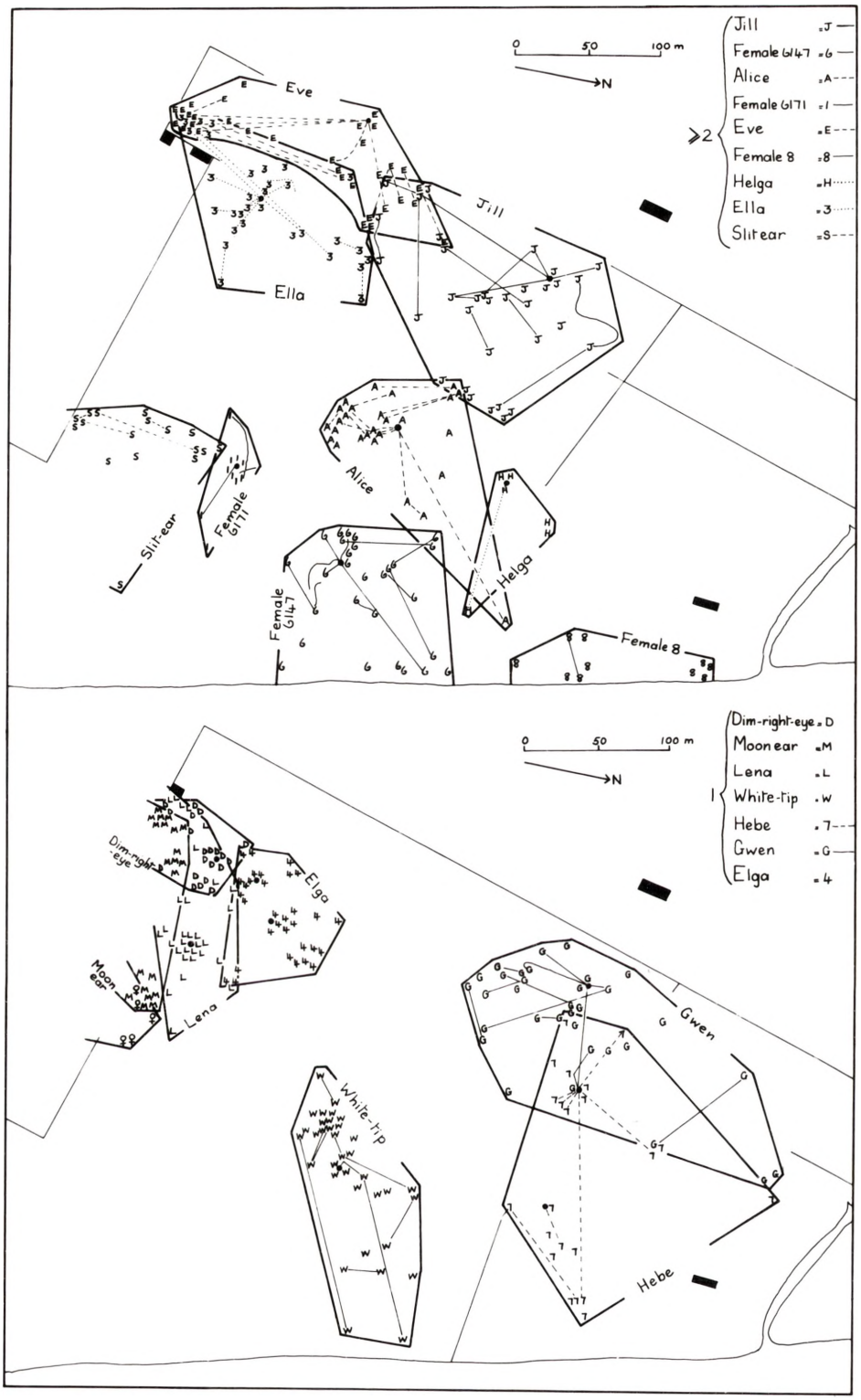


Figure 6.11 : Home ranges of all females for Jan. - Apr
(inclusive), 1968. a) upper - 2 yrs old
and over by the end of April.
b) lower - less than 2 yrs, more than 1 y

The first third of 1968 showed little change in the home ranges of the females (Figure 6.11a and 6.11b). Gert had disappeared late in November 1967 (not long after Hester), and Jill had expanded her home range to include Gert's den. Both major dens in Jill's and Jess' home ranges had collapsed early in September of 1967, and this had coincided with Jess' disappearence at the end of August 1967. After the loss of these dens Jill had expanded her home range to the east and all observations of her at the north east and south east extremities of her home range in 1967 (Fig. 6.10a) occurred after August, including the use of a den in this area. Jill was obviously exploring the area in an attempt to find a new den. When Gert disappeared at the end of November 1967 Jill apparently took over Gert's den, because on the 1st January, 1968 Jill was trapped at the base of Gert's den tree and on the 23rd January she was seen to emerge from the den. Although Jill continued to be seen at the south western end of her home range until the end of the observational period in April, most observations were made at the northern end of her old home range and in the area previously occupied by Gert.

Ella had apparently become an established female with very little overlap with her mother's (Eve) home range. Female 6147, Female 8, Alice and Helga all had proportionally large exclusive areas. Helga disappeared towards the end of January and the one observation of Alice at the north eastern extremity of her home range (responsible for the overlapping of their home ranges) took place on 7th March i.e. a month after Helga was last seen.

Of the younger females (2nd year) Female White-tip had established herself in a den formerly used by Alice and was most frequently seen between the areas usually frequented by Alice and Female 6147 (her mother). Gwen and Hebe were the daughters of Gert and Hester and appeared to have taken over the areas vacated by their mothers. Gwen, however, did not take over her mother's den but moved to one of the dens formerly used by Hester, apparently having been displaced by Jill.

At the south western end of the study area several home ranges of

Table 6.12

Origin of juveniles that established or attempted to establish home ranges within the study area. Py = pouch young

	Male	Age at 1st observation (months)	Female	Age at 1st observation (months)
Origin known	Jim	Py	Jess	Py
			Gwen	Py
			Helga	Py
			White-tip	Py
			22	Py
			3	Py
			24	Py
			79	Py
			19	Py
			18	Py
			Iara	Py
			23	Py
			71	Py
			42	Py
Total No.	1		14	
Origin unknown	32	(15) 19	Dim-right-eye	10
	33	22	73	19
	22	19		
	56	11		
	64	25		
	26	>16		
	15	11-13		
	20	8-9		
	16	18		
Total No.	9		2	
Grand Total	10		16	

females in their second year occurred, with a considerable amount of overlap of home ranges apparent. Nevertheless on closer inspection of actual sightings the overlap was not in fact very great. Actual overlap was greatest at the sheds right in the south west corner of the study area, where possums from all around converged on the cattle feed that was nearly always available. Elsewhere the overlap was more a result of the draughting method or of an infrequent excursion by one female into another female's home range. For example Dim-right-eye's activity centred on her den about 35m to the south of Ella's den and only once was Ella seen near the base of the younger female's den tree. Lena had an exclusive area round her den and actual overlapping observations with Ella and Dim-right-eye were relatively few. The other two young females, Moon-ear and an unmarked one, centred their activity to the south and were seen in the study area only at the sheds and in a small area to the south east of Lena's home range. Elga was Ella's daughter and although by the end of April she was only just 12 months old she had moved to her own den tree and had maintained a consort relationship with Male 22. Her home range, however, was still completely overlapped by that of her mother.

It is apparent from these observations that a female's home range becomes more exclusive in relation to other established females, as she grows older. An established home range of this sort appears to be attained by the end of a female's third year, although this may occur earlier if there are no older established females in the area. The home ranges of younger females, mainly those in their second year, may overlap the home ranges of older females, usually their mother's.

6.5 DISPERSAL OF YOUNG AND HOME RANGE ESTABLISHMENT

Dispersal of the young possums after gaining independence from their mothers, differed for the sexes.

Young females who established themselves in the study area were daughters of females living in the area (Table 6.12). Only two were of unknown origin and one of these (Female 73) was thought to be the daughter of Female White-tip. The other (Female Dim-right-eye) was a peripheral

female whose mother may have lived just outside the study area.

Young males on the other hand, showed the reverse pattern (Table 6.12). Only one young male (Jim) who was born in the study area, established a home range of his own in the area. He did, however, undergo a dispersal phase because his newly established home range was not adjacent to his mother's. Conversally nine out of the ten young males who attempted (not all successfully) to establish home ranges in the study area were of unknown origin and presumably came from outside.

Table 6.13

Juveniles born in the study area, but disappeared before establishing a home range in the study area. Cases of pouch mortality (2 males only) not included.

Male	Age at last observation (months)	Female	Age at last observation (months)
Gerald	16	10	14
(8)	13 (18)	Gina	8
14	11	17(c)	7½
13	10	+30	7
Andy	9	+17(t)	5½
43	9	6148	5½
4	8		
+4th left toe	7		
+4th right toe	5½		
Total 9		6	

+ Still dependent when disappeared

Nine of the fifteen possums born in the area, and who disappeared after emerging from the pouch, were males.

When young which disappeared before attaining independence (i.e. inferred mortality) are discounted the difference between the sexes becomes significant (Table 6.13). Together with the evidence for strange males moving into the area, and the lack of evidence of similar female movements, the disappearence of young males is attributed mainly to dispersion, whereas the disappearence of young females is attributed mainly to mortality.

6.51 Females

Three case histories are given to illustrate the dispersal and

establishment of young females.

Case 1: Ella, daughter of Eve

Agonistic behaviour was first observed between mother and daughter when Ella was 246 days old, (8 months), but she continued to share her mother's den until at least 326 days (10¾ months) old. Ella by this time had a joey of her own, born when she was 300 days old. The last observation of Ella sharing a den with her mother involved an agonistic interaction in which Eve displaced her daughter from the den at dawn, but the latter re-entered it soon afterwards. Fourteen days later Ella was observed using a separate den for the first time, in a tree about 20m from the maternal den tree. Presumably she had finally been ejected from the maternal den by Eve.

By the time she was 14 months old Ella had begun to use a den (T88) on the north western periphery of Lesley's home range (see Figures 6.9 and 6.10). Within 10 days of first being observed to use den T88 Ella had two agonistic encounters with Lesley on two separate nights. Although Lesley was never observed to use den T88 she twice chased Ella out of the tree soon after dusk. In the second encounter Lesley was seen to climb T88, soon after emerging from her den about 40m away, to chase Ella down the tree and to continue the chase for 30-40m on the ground. However, Ella continued to use den T88 until 24 months old. At 22 months of age she began to visit the dens formerly used by Lesley, who had disappeared when Ella was 21 months old. She was twice seen using den T96, one of Lesley's dens, when 28 and 29 months old but by the time she was 30 months old she had taken over den Mt12, Lesley's main den. From then until the end of the study when she was 43 months old she was seen using this den only and to have established a home range as shown in Figure 6.11.

Case 2: Jess, daughter of Jill

To the age of 210 days Jess had a contact relationship with her mother, but when next observed at 248 days (8 months) the mother-joey

bond had completely broken down. They were by then using separate dens although at 288 and 294 days they were seen to share a den for the last time. Jill had two main dens which she alternated in using, and Jess continued to use one of these up to the age of 10 months. At 10 months she was first seen using a new den (T92), but still in Jill's home range. She continued to use it fairly consistently up to the age of 18 months, except for a brief period of about 1 month when she used T88 when 13 months old (3 months before Ella used this den), and two observations when she used two dens well outside her maternal home range. Finally she settled into using one of Jill's main dens and continued to do so until she disappeared at 29 months which coincided with the fall of the den.

Before Jess moved into den T88 Jack had been using the den, but was apparently displaced by Jess. It was displacement rather than a voluntary move on the part of Jack as shown by the following observation. Jack returned to den T88 just before dawn to find Jess already in the den. There was an agonistic interaction and Jack left the tree soon after. He then climbed up to Eve's den but was displaced by another possum (presumably Eve). So he finally climbed a third tree and entered a den rarely used by any of the possums in the area. Over a period of five days (3 obs) he was seen to use the last den and another den in the area, also one rarely used. However, on the sixth night both he and Jess emerged from den T88, this being the last observation of Jess using the den. After Jess ceased to use T88 he apparently continued to use it because the next observation of him coming out of a den was from T88. Soon afterwards, however, he shifted to den Mt12. There was no agonistic behaviour observed when both Jack and Jess came out of den T88 but Jack followed Jess down the tree and continued to follow her on the ground apparently sexually attracted to her. It was not known whether Jack's presence induced Jess to return to using den T92.

The two dens which she used outside her maternal home range

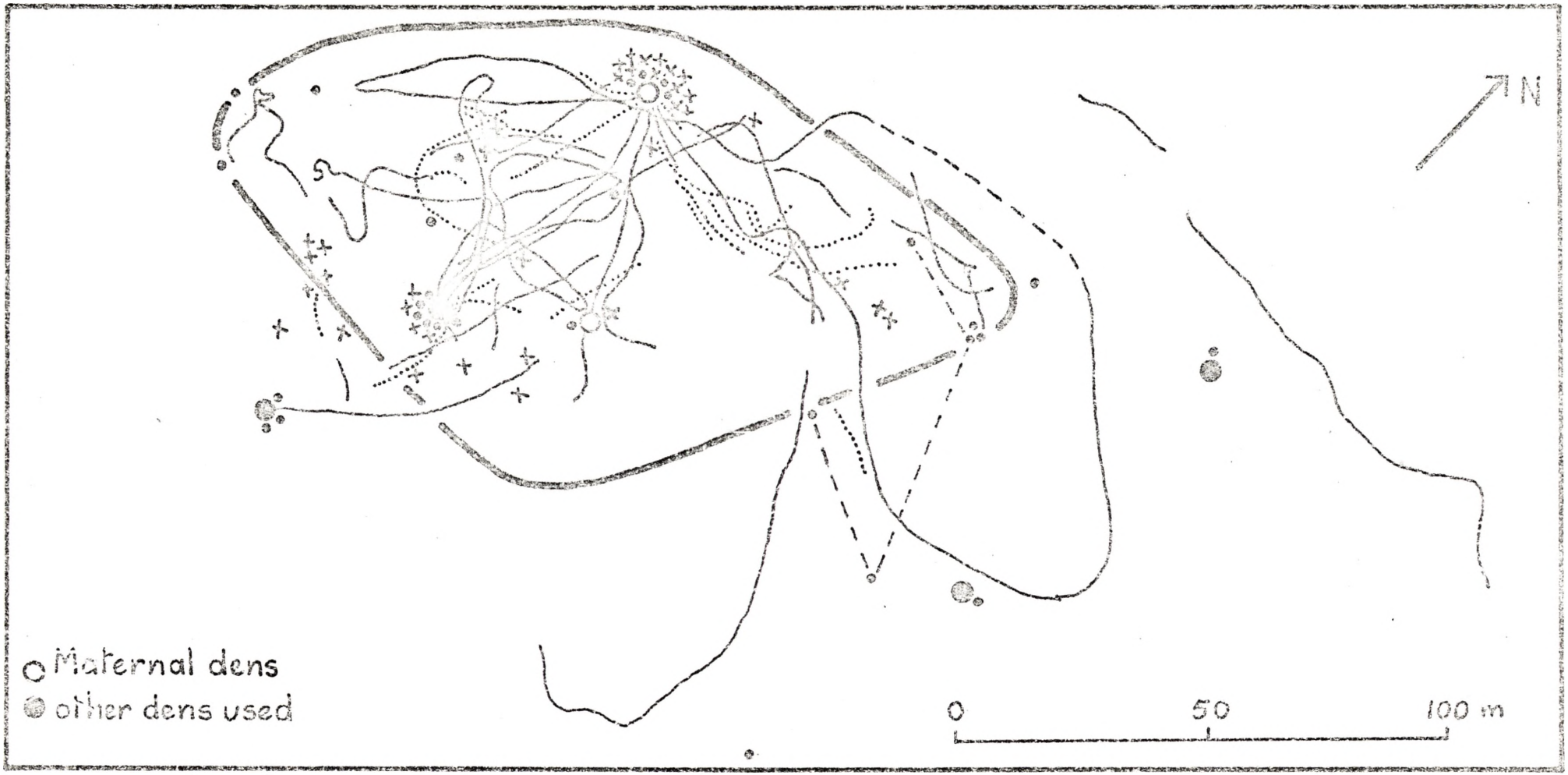


Figure 6.12 : Observations of Jess from the age of 9 months, when she became independent, to 27 months when she disappeared. Dots and continuous lines = observations from 9 to 17 months; x and dotted lines = over 17 months; heavy line = mother's home range.

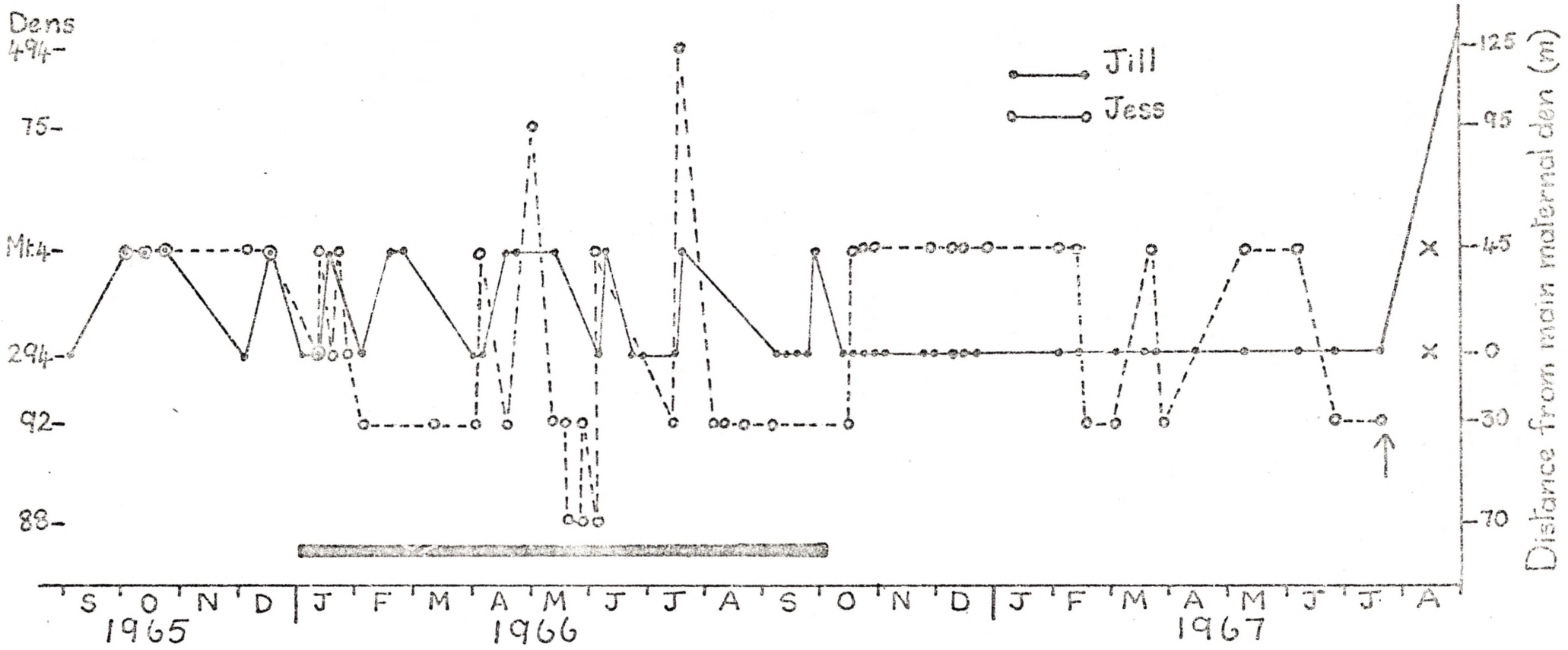


Figure 6.13 : Use of dens by Jill and her daughter, Jess, until Jess disappeared (last obs arrowed). Heavy line Jess' exploratory phase (9 - 17 months), see also Fig. 6.12; x = approximate time den destroyed.

were den T75, (one of Alice's main dens) at the age of 13 months, and den T494 (a den used by Alec) at 15 months. All her movements well outside and to the east of her maternal home range (Fig. 6.12) took place between the ages of 9 and 17 months, after which her movements became based on one of Jill's main dens and her home range contracted to that shown in Figure 6.10. The use of several dens before settling down to using predominantly one den, and the exploratory movements well outside her maternal home range indicate that Jess went through a distinct exploratory phase between about 9 and 17 months.

A number of agonistic interactions between Jess and her mother were observed. The first two at 13 and 15 months of age were simple give-way interactions won by Jill. In the third (also at 15 months) Jess was sitting outside Jill's den entrance before dawn when Jill arrived. They sat staring at each other, and it was Jess who suddenly rushed at Jill. Jill at first hurriedly gave way, but suddenly the situation reversed and Jill chased her daughter down the tree. When 18 months old Jess was seen to give-way to Jill once and to be chased by Jill once. However at 19 months the series of fights won by Jess (Ch. 5.4) took place on 15th October. Jess had emerged from den T92 on the evening of these fights, and had returned to den Mt4, one of the main dens in Jill's home range, at dawn. From that time on until she disappeared, Jess used this den, with the occasional return to T92 (Fig. 6.13). Whether or not the switch to den Mt4 actually took place for the first time that night, it is probable that a reversal of dominance allowed Jess to take over one of the main dens and to establish herself in the maternal range. No further agonistic interactions were observed between Jill and Jess.

Case 3: Gwen, daughter of Gert

A change in the mother-joey relationship from a contact to no contact one occurred between the age of 225 and 261 days. However, Gwen continued to share Gert's den until she was 350 days (11 months)

old, by which time Gert's next joey had begun to ride on her back. When 13 months old two agonistic interactions occurred between them and by 14 months Gwen was using a separate den, although in the same den tree, and avoiding her mother. This was still the situation a month later when Gert disappeared.

However, Jill took over Gert's den tree almost exactly a month after Gert had disappeared. This coincided with Gwen's shift to another den 35m away where she established herself. Later when Gwen was 25 months old Jill disappeared, and within 12 days of the last observation of Jill (made as she came out of her den) Gwen had returned to her former maternal den and reoccupied the den left vacant by Jill and continued to use this den exclusively until the end of the study 2½ months later.

The three case histories appear to be typical of the dispersal of young females and the establishment of their home ranges. All three established a home range which either overlapped or were adjacent to their mother's home range. This was the general pattern for the young females who managed to establish themselves in the area as indicated by the Figures 6.9, 6.10 and 6.11. The exception was Female Slit-ear who first attempted to establish a home range in 1966 adjacent to her mother's (Female 6230) but then disappeared. She reappeared however in 1968 (Fig. 6.11) to the south east having presumably first moved to an area just outside the study area. Her establishment of a home range was not adjacent to her mother's home range as observed, but the distance moved was not great ($<$50m).

Young females when displaced from the maternal den have to find a new den and in many cases they use dens apparently not favoured by the older females. These dens are either too small to accomodate a fully grown animal, or are not favoured by older females possibly because they are too low or too exposed. It is the young animals who also open up den dens. Although possums do not build nests they can modify existing cavities. Female 10, when about 6½ months old and still sharing her mother's den, was observed to do some excavating of a hole just before returning to her

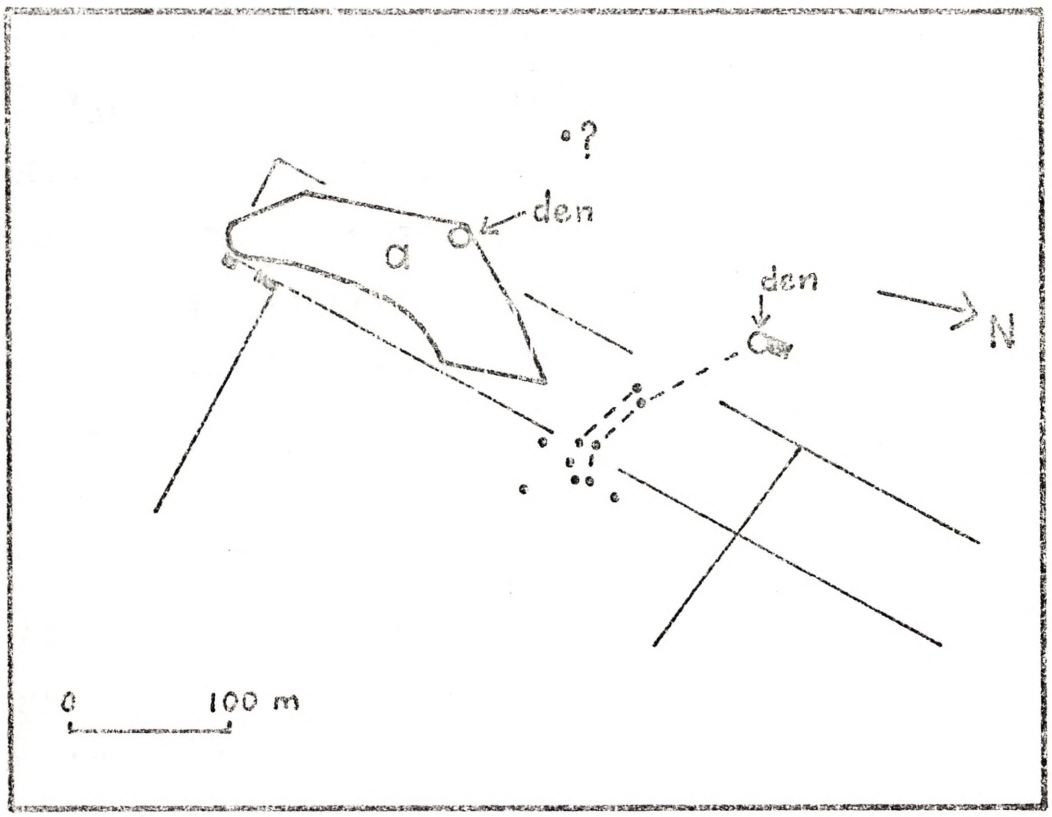


Figure 6.14 : Eve's shift of home range a = Eve's home range until April 1968; ? = unconfirmed observation between April 1968 and Jan. 1969; dots and dashed lines = observations Jan.-Sept. 1969.

mother's den at dawn. She first pulled lumps of mud out of a hollow part of a dead branch, then squeezed into the hollow until just her hindquarters were left dangling out of the entrance. It was such a tight squeeze that I thought she had become stuck. Eventually, however, after a considerable struggle she managed to gain a foot hold with her back feet and pulled herself out. Helga at the age of 14 months was first seen using a den away from her maternal area. Before she emerged from the den on the first observation she could be heard gnawing wood inside the tree for 2-3 min presumably as she enlarged the den. Possums had not been seen using this den before.

The usual pattern of home range establishment was for the young female to leave the maternal den and initially to take up residence in another den either within, or adjacent to the maternal home range. This is followed by a number of moves to other dens until the female settles in one in an exclusive area of its own. However, apart from Jess, there were two other young females who apparently displaced their mother from the maternal den. The best documented case being that of Emily who was a daughter of Eve. Emily was observed sharing her mother's den when she was 11 months old, and both were still using the maternal home range and presumably the maternal den when Emily was 12 months old. Following a 4 month break in observations Emily (now 16 months old) was still using the maternal den, but Eve had disappeared, presumed at the time to have died. However, 8 months after she was last seen Eve reappeared, now using a den in the ceiling of a shed to the north of her original home range and with no overlap with her former home range (Fig. 6.14). During the period of Eve's absence I made one unconfirmed observation (at the time discounted) of her in a tree at the western boundary of the study area. Up to the time of her disappearence Eve had consistently used her original den for 2½ yrs, and by the time she moved it was the only den in her home range i.e. she was well established. I had not observed any agonistic interactions between Emily and Eve, but bearing in mind the reversal of dominance between Jess and Jill, the most likely explanation was that Eve

was displaced by her daughter.

The second example was that of Alice and her daughter Amy. To the end of April 1968, Alice's main den had been T75 with also fairly frequent use of T48 until September 1967, when that den was taken over by Female White-tip. Up until April 1968 Alice and her daughter (by then 12 months old) frequently shared a den. When observations started again 4 months later it was Amy who was consistently using den T75 and Alice was seen using dens T496, T494 and T73. All these dens were in Alice's former home range but she had rarely used them before. Again it would appear that a daughter between the ages of 12 and 16 months had displaced her mother from the maternal den.

It may be significant that the age of Eve and Alice when displaced were 5 and 6 yrs respectively. Similarly when Jess took over one of Jill's main dens, Jill was 6 yrs old. The estimated age of the oldest female in the study area was 7 years 7 months (Jill when she disappeared). Thus the mothers who were displaced by their daughters were approaching the upper age limit for females in the field and may have been suffering from the onset of senility.

6.52 Males

The age at which young males disperse from the maternal home range varies from 7 to 16 months (Table 6.13), although those disappearing at 7 and 8 months may be the result of mortality rather than dispersal. The example of Male 43, (son of Female White-tip) is the best documented case of one of the earlier disappearances presumably due to dispersal. There was an abrupt and total break down of the mother-joey bond when he was 7 months old, and he began to use two separate dens, but still within his mother's home range (Chapter 5.617). One of these dens was a hollow spout of a dead limb with a diameter barely large enough for the young male to enter and was only ever seen to be used by young possums who had not attained full size. The other was a recently formed opening (by natural decay), only 1½m from the ground, into a spacious cavity at the base of the maternal den tree. Male 43 continued to use these until he was just

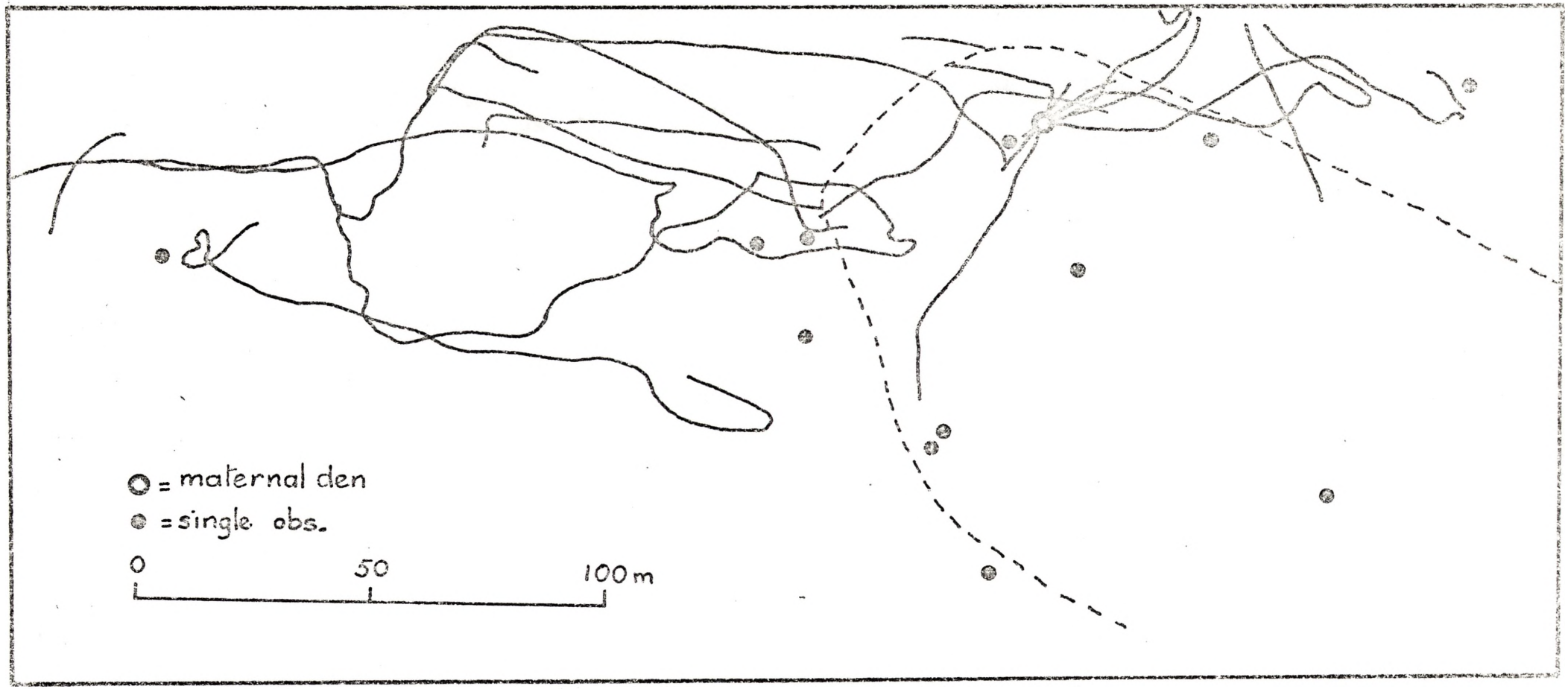


Figure 6.15 : Observations of Gerald from the age 10 months until he disappeared at 16 months (closed circles and continuous lines), in relation to his mother's (Gert) home range (broken line).

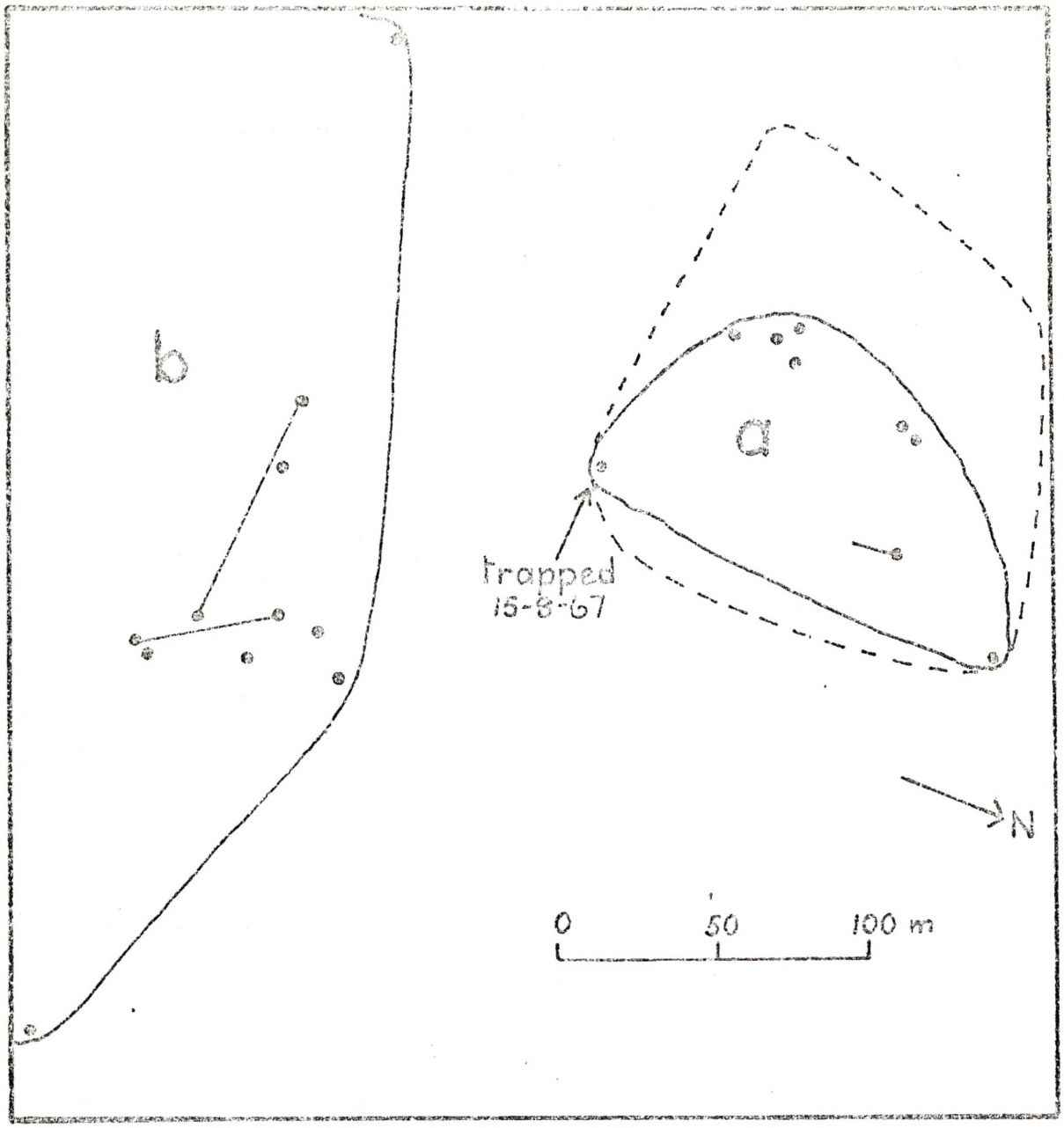


Figure 6.16 : Observations of Jim (dots) in relation to his mother's (Jill) home range (broken line). a = observations up to the age of 9 months; b = observations between the ages of 12 months and 17 months.

9 months old, then disappeared. By the time he disappeared he was seemingly completely independent of his mother. Neither of the dens he was using were very suitable, one being too small, the other with an opening too close to the ground and this may have been responsible for his early disappearance, possibly through dispersal.

The oldest juvenile male known to be still using the maternal home range was 16 months. This was Gerald who continued to use the maternal den tree (Mt3) which contained several dens. He was first observed using a separate den (in the maternal den tree) at 246 days (8 months) but was also seen emerging from the same den as his mother at 474 days which was 25 days before he was last seen. From the age of 10 months he began to extend his movements to the south west, well outside the maternal home range, and was frequently seen in this area until he disappeared (Fig. 6.15). Male 14 was first seen outside the maternal home range at 344 days (11 months). This was also the last observation of him. These movements indicate that a young male may start exploratory movements outside the maternal home range at about the same age as a young female (see Jess). However, the male exploratory phase almost certainly lasts longer.

Another young male (Male 8) was infrequently seen in his mother's home range up to the age of 13 months. He was seen once more, at the age of 18 months, at least 340m south of his mother's home range, indicating that he had dispersed between the ages of 13 and 18 months.

Jim was the only male born in the study area to also establish a home range in the study area. He was still following his mother (Jill) at the age of 251 days (8 months), then at 279 days (9 months) he was trapped at the south eastern corner of his mother's home range. He was next seen at 367 days (12 months) to the south in the area where he established himself (Fig. 6.16). This represented a shift of 150m from the periphery of the maternal home range or 100m from the expanded side of Jill's home range following the loss of her main dens.

Jim's successful establishment in his new home range was confirmed by observations made on two separate nights during September 1969 when

Jim, now 34 months old, was seen in this area. Also during these observations Male 72 (15 months old), who was Emily's son, was seen down by the river at least 370m from his maternal home range. These observations indicate that a young male may establish a home range as close as 100m or travel at least as far as 370m from the maternal home range.

The discrepancy between the ages of young males last seen in the maternal home range (Table 6.13) and of strange males first seen in the study area (Table 6.12) is small and attributed to inadequacies in observations. It was unlikely that I saw a young male on the last night in his maternal home range or that I caught an incoming male on his first night in the area. An extreme case of this is shown by Male 32 who was first trapped when 19 months old, 4 months after a young male (presumed to be him) had been first seen in the area. The age of males dispersing from their maternal home ranges therefore, would probably be between 8 and 16 months.

Males who came into the area at an older age e.g. Male 33 at 22 months and Male 64 at 25 months were probably in the process of adjusting their home ranges, in the same way that Male 9 adjusted his home range from 1966 (Fig. 6.6) to 1967 (Fig. 6.7).

Examples of young males moving into the study area are given in the three following case histories.

Case 1: Male 32

A young male presumed to be Male 32 was seen 4 times in the vicinity of Jack's den in Mt3. Male 32 would have been 15 months old when first sighted. A month later Jack disappeared leaving a vacant den in Mt3. At the age of 19 months Male 32 was seen to emerge from a den in Mt3, and from then until the end of the study, when he was 30 months old, he used one or other of the dens in Mt3 with only the occasional use of a den in Alec's home range when Alec and Male 32 were acting as primary and secondary consort males to Alice.

Case 2: Male 22

Male 22, who had a distinctive scruffy tail, was first seen 8 days before being trapped at an estimated age of 19 months in December 1966. He was seen using den T934 twice during the first month (Fig. 6.6b), but early in 1967 (Fig. 6.7b) he shifted his centre of activity to the west, first to Mt12 but finally settling down in den T195 (a den not previously seen to be used by a male), where he acted as a secondary consort male to Ella and a primary consort male to Elga in 1968.

Case 3: Male 16

He was first caught at the south west corner of his home range (Fig. 6.7b), at the age of 18 months, the day after Gus was accidentally killed. Within the next five days he was seen twice in the general vicinity of the vacated home range of Gus, and a month later he was seen coming out of Gus' den. However, seven days later he was seen emerging from a den in Alec's home range. He continued to use this den for a further month until he disappeared from the study area. As Jack expanded his home range to fill the vacancy left by Gus (Fig. 6.7a), it is possible that Male 16 was displaced from Gus' den by Jack.

Both Male 32 and Male 22 were successful in establishing a home range. Both acted as secondary consort males and were more active than older males (Chapter 5.214). Male 16 on the other hand was unsuccessful.

6.53 The Role of Resident Adults in the Dispersal of the Young

Evidence presented in the section on mother-joey relationships indicat that the development of aggressive behaviour by the mother plays a role, possibly a decisive one, in causing the young possum to leave the maternal den. Although in some cases it was the mother who left and the daughter who stayed in the maternal den. The age at which a joey finally leaves the maternal den can vary from as early as 7 months if an abrupt break down of the mother-joey bond occurs, to as late as 17 months if the break down of the mother-joey bond was of the gradual type. Despite the different pattern of dispersal of males and females there was no significant

Table 6.14

Age at which juveniles were last seen sharing a den with their mother. Records of juveniles younger than 210 days not included.

	Age of juveniles (days)	
	Female	Male
	306	229
	226	247
	311	219
	211	295
	227	474
	228	280
	226	251
	350	336
	331	
	335	
	523	
	350	
	209	
	295	
No.	14	8
Σx	4128	2331
Mean	294.86	291.38,
Σx^2	1311564	727409
Variance	6742.43	6062.73
St.dev.	82.11	77.63
S.E.	21.95	27.45

Analysis of variance

Source of variation	d.f.	S.S.	M.S.
Among sexes	1	61.729	61.7289 F = 0.0087
Residual	20	142607.589	7130.3993 p > .75n.s.
Total	21	142669.318	

difference detected in the age they were last seen sharing a den with their mothers (Table 6.14). The two oldest juveniles seen to be still sharing a den were Gerald at 474 days (15 months) and Amy at 523 days (17 months). In addition, if Male 6214 was Alice's son, the sharing period extended in this case to the age of 30 months. It was not known why there was this considerable variation in the age at which juveniles left the maternal den but it may depend on the size of the den, the presence of other dens in the maternal home range, and individual variation in the behaviour of the mothers. Alice, for example, showed a tendency to share her den for longer periods with her joeys and also to share her den with older males (Male 6214, and Alec). On at least one occasion four possums were seen to come out of her den: Alice herself, an independent juvenile, a dependent joey, and Alec. She was the shyest of the females in the area and this may have been linked with a greater tolerance to other possums.

Although no significant difference could be detected between the ages at which males and females last shared their mother's den, a significant difference was detected in the proportion of agonistic interactions that occurred in a den tree and elsewhere between a mother and her male and female offspring up to the age of 16 months (the age at which the oldest male left the maternal den) (Table 6.15).

Table 6.15

Agonistic interactions between mother and offspring to the age of 16 months. Numbers in parenthesis are the numbers of give-way interactions: chases and fights

	Sex of offspring		
	Male	Female	
No. of mother-offspring pairs	4	10	
In den tree	13 (7:4)	12 (9:3)	25 (16:7)
Elsewhere	3 (1:2)	20 (13:7)	23 (14:9)
	16 (8:6)	32 (22:10)	48 (30:16)

$G = 6.834$ 1 d.f. $p < .01^{++}$ (Yate's correction used)

A mother's agonistic interactions with her male offspring occurred pre-

dominantly in a den tree and were presumably concerned mainly with the use of the maternal den. Once away from the den tree a female apparently took very little notice of her male offspring, although the three interactions that did take place away from the den tree were relatively aggressive (even the give-way was a definite supplanting interaction by the female). Her interactions with her female offspring, on the other hand, occurred predominantly away from the den tree.

The behaviour of a resident adult male towards a juvenile female is neutral until she becomes sexually attractive, presumably when she first comes into oestrus, then there is a period of transition in the relationship until the female becomes mature (Chapter 5.722). His interactions appear to have no bearing on the dispersal of the young female except where there is a conflict for dens as was the case between Jess and Jack over den TS8. No other observations were made involving direct conflict between adult males and juvenile females, but there is a period when a young female is nervous of a male and should the conflict over a den occur during this period it is possible that the male would displace the young female from the den.

Interactions between adult males and juvenile males raised in the adult's home range were observed eight times, seven of them being give-way interactions. In one of the latter interactions the adult male gave way at a den (Chapter 5.721), but in the other six the juvenile male gave way to the adult who apparently took no notice of the juvenile. Only in one interaction did the adult male chase and bite at a juvenile's rump. This occurred between Gus and Gerald when the latter was 13 months old. Gerald also had two encounters with resident males when he extended his movements beyond the maternal home range to the south. At 11 months Jack climbed into a small tree that Gerald was in and supplanted him but did not chase him. Two months later he and Victor had an encounter, possibly a short interrupted chase, on the ground, and won by Victor.

Interactions between resident males and young males of unknown origin were observed more frequently. Of the 16 interactions observed, 14 were of

an aggressive type (1 fight, 9 chases, 4 supplanting give-ways) and only two were non-supplanting give-ways.

Despite the lack of observed aggressive encounters between a resident adult male and a juvenile male raised in his home range, it is probable that adult male aggression is responsible, partly if not wholly, for juvenile dispersal. This was most clearly seen in the interactions between an adult resident male and young males in the early stages of attempted home range establishment.

6.6 TERRITORIAL ASPECTS OF HOME RANGE

Taking Pitelka's (1959) definition of a territory as an exclusive area, both male and female brush-tail possums show a marked tendency to become territorial. Individuals of either sex who are successful in establishing a stable home range do so with a definite exclusive area relative to other well established individuals of the same sex. In both sexes however, home ranges, including the exclusive areas of older establish individuals, may be completely overlapped by the home ranges of younger establishing adults.

Dens are an important focal point in an individual's home range, occur in the exclusive area, and certainly within the core area of the home range. Den trees are the only areas *per se* which are defended from other individuals of the same sex, especially in the case of females (Ch. 5.4). Dens themselves are also the focus for male-female non sexual interactions, but a tree with more than one den may accomodate both an established male and female but not two adults of the same sex.

Despite the remarkable lack of overlap between individuals of the same sex of the six central individuals in 1966, there was no evidence that a definite boundary existed. Olfactory marking was concentrated at den trees and to a lesser extent at focal points in the vicinity of an oestrous female (Ch. 4.23111). Otherwise it occurred irregularly throughout the home range with no evidence that it was concentrated along the boundary of the home range (Ch. 4.2314). However, there was some evidence that olfactory marking was concentrated at certain trees other than den

trees. Similarly there was no evidence from movements of the six central individuals in 1966 that a boundary was patrolled, nor was there a track system on the ground which one might expect if this was so.

Female home ranges are smaller than those of males, because it is the female who determines the use of dens in an area and it is the male who is the active partner in the sexual relationship. In theory, therefore, a female's home range need contain only a den and sufficient food to satisfy her resource requirements. A male's home range on the other hand must contain not only an available den plus food but also a female. Males need to travel to find a female (the sharing of dens being rare). As a result males have larger home ranges. Congregations of males at an oestrous female results from considerable excursions outside their core area and permits considerable overlapping of their home ranges.

6.7 DISCUSSION

It is concluded that the dispersion of brush-tail possums is a territorial arangement based on a defended area which is a den tree. It is considered that this arrangement functions in the following way. All things being equal, an individual will each night use an area where the probability of meeting a dominant individual of the same sex is lowest. Individuals learn to avoid another individual of the same sex through direct interactions or through indirect means, such as vocalisations, but more especially via olfactory cues and a greater density of them in an area which it visits more frequently. These olfactory cues may be the result of olfactory marking, such as chinning and chesting, but it is also possible that individuals can detect the passage of another individual from the scent of its foot prints. Providing individual recognition of scents occurs, a possum travelling through an area will have some measure of the probability of meeting another individual and of that individual's dominance status. Dominance is learnt through actual encounters which are concerned with the establishment of the relative dominance between two individuals rather than the defence of an area per se. This is supported by the fact that short term reversal dominance connected with area was not observed nor were long chases common.

Where individuals are of equal status in respect to dominance mutual avoidance will be the greatest with the development of definite exclusive areas. Where there is a pronounced difference in the relative dominance between two individuals of the same sex the dominant animal of the pair may take little notice of the other and it will be the subordinate animal who will take the avoiding action. Therefore those individuals which are the lowest in the hierarchy (the youngest individuals) will seek to avoid all other individuals of the same sex. The dominant animal can virtually ignore the subordinate animal as it poses no 'threat' to it, and the subordinate individual can use the home range of the other providing it takes avoiding action.

Older males and females have exclusive areas relative to other members of the same sex and dominance status, and a young subordinate individual can have a home range that may totally overlap that of an older individual. Subordinate individuals by attempting to avoid dominant individuals will gravitate to dens and areas not used by established individuals.

At focal points, such as food concentrations and oestrous females, overlapping of movements will be greater and agonistic interactions may result.

The pattern of extensively overlapping male home ranges, but with an exclusive area, and the smaller, but none the less clear territories of the females, at first sight appears to be in conflict with Dunnet's (1956 and 1964) findings at Canberra. However, a closer examination of Dunnet's data reveals that the differences between the Canberra and Moggill Farm populations are not real.

Dunnet (1964) concluded that males had territories with very little overlap, apart from his area V where one male completely overlapped the "territories" of two other males. Most of the overlap in the home ranges of the established males at Moggill Farm was the result of long movements by males when they converged on oestrus females. Since, during these movements males did not feed, the probability of their entering traps would

be low. Therefore the estimation of home ranges from trapping data alone, as in Dunnet's studies, is likely to miss such movements, which were responsible for the overlap of male home ranges at Moggill Farm. The observations of male dispersion in Dunnet's (1964) area V is probably an example of an established male and two establishing males, because the "dominant" male was significantly heavier (3225g) than the other two males (2000, and 2275g), suggesting that the dominant male was a mature male, whereas the other two were relatively young.

If one examines the dispersion of females in Dunnet's area I (1956) and I-II (1964) where the greatest density of females occurred, it is apparent that females did in fact have exclusive areas. This becomes clearer when yearling females (No. 13 in 1956, and nos 92, 81 and 410 in 1964) are ignored. The only areas where females may have lacked exclusive areas was around the homestead itself in area I-II (1964). However, one of the females (81) shown in Figure 7 was a yearling, and for the other seven females the scale is too small to plot all their home ranges. The homestead area is akin to the area with the sheds in the south west corner of the study area at Moggill Farm, where both males and females converged on the food available, but had small exclusive areas in the vicinity of their dens. It is possible, therefore, that the homestead area would show a similar dispersion of females, but such an intricate pattern is not likely to be revealed by trapping alone.

In New Zealand Crawley (1973) found that trap-revealed home ranges of individuals of the same sex overlapped almost totally, with multiple overlapping occurring in most cases, in his Crongorongo population. The density of possums (10.6/ha) was over three times that of Moggill Farm (2.2/ha), and home ranges of adults were smaller (males 0.81±0.05 ha, females 0.46±0.04 ha) than at Moggill Farm (males 3.71 ha, females 1.74 ha). It would appear that neither males nor females in the Crongorongo population were territorial. Batchelor et al (1967) present evidence based on removal trapping that at densities of over 5/acre (12.4/ha) the percentage kill rate is much greater than expected from the increased density, and they

attribute this fact to the breakdown of territories which allows individuals to move into areas vacated by killed individuals much faster than if a territorial system was functioning. Also it is at about 12/ha that Kean (cited in Batchelor et al 1967) considers that territorial marking patterns and social restrictions on movements break down.

Dispersal of young at Canberra (Dunnet 1964) was similar to that at Moggill Farm. A greater number of females (five) than males (one) remained to breed in their native area, and young animals disappeared from their native area when six months to one year old. Similarly in the Orongorongo population seven of the eight young possums that settled in their native area were females (Crawley 1973).

Differences between the Moggill Farm population and Dunnet's Canberra population were slight and could be mainly attributed to the different techniques used and different interpretations of the data. In the New Zealand populations with much greater densities, there is some evidence to suggest that dispersion of individuals is significantly different, perhaps with the breakdown of territoriality to the extent where exclusive areas can no longer be maintained. However, the New Zealand studies were large-scale population ones based on trapping, and a more intense study of movements and behaviour is needed before these differences are substantiated.

CHAPTER 7

GENERAL DISCUSSION

7.1 The Social Organisation of the Brush-tail Possum

The social organisation of the brush-tail possum is essentially solitary. Individuals are usually found alone both when active at night and when resting during the day. The only period in which social attraction is evident is in the breeding season. A consort pair exists for about one month prior to mating, but does not extend beyond mating. Young may share the maternal den until about 17 months old but usually leave earlier.

In the open forest of Moggill Farm dispersion was centred on dens found in eucalypt trees (Ch. 6.3). Without such a den it is probable that a possum is unable to establish a home range because the open canopy of a eucalypt tree provides no protection. Adult possums of the same sex did not share the same den, and den sharing by male and female was rare (Ch. 6.3). A den is the only object defended in the classical sense of territoriality, and forms a territorial nucleus to the home range of a possum.

Adult females were always dominant to males in interactions concerned with dens (Ch. 5.23), thus it was the female who determined the use of dens. Although females did not share the same den tree, males were tolerated in the den trees of females. Thus dens in trees with more than one den (10 to 15% at Moggill Farm, Fig. 2.2) were available to males. A female may have more than one den tree and a resident male could find a den unoccupied by the female at the time, returning to it later than the female and so avoiding eviction by her (Ch. 6.3). Adult males were often dominant to juvenile females at the time when the young female was beginning to seek a den of her own (Ch. 5.722).

Beyond a den tree there was no evidence that a possum defended an area. There was no patrolling (Ch. 6.2) or olfactory marking of a boundary (Ch. 4.2314). Nor was there dominance reversal (Ch. 5.33 and

5.4), which is characteristic of defended territories. Home ranges of males and females completely overlapped in two superimposed and independent patterns. There was no evidence that a pair maintained a common home range except by coincidence. Between individuals of the same sex and status, exclusive areas within a home range existed (Ch. 6.4). Females had smaller home ranges than males (Ch. 6.2). Where dens were well spaced the home ranges of established adult females did not overlap (e.g. the cases of the central females Jill, Gert, and Alice. Fig. 6.4), and the whole home range may in fact be exclusive. Where dens were closer (e.g. in the south-west corner of the study area) considerable overlap of home ranges occurred, but a small exclusive area was still observed in the immediate vicinity of the den tree (Ch. 6.42). Similarly male home ranges contained exclusive portions and much of the range overlap was the result of extensive movements made to oestrous females for the purpose of mating. Occasionally a pronounced dominant-subordinate relationship existed between older animals with almost complete overlapping home ranges as in the case of Donald and Jack (Ch. 6.41). The home ranges of subordinate individuals, usually young animals, were completely overlapped by those of established adults (Ch. 6.4). Subordinates who were successful in establishing a home range with an exclusive area usually did so by the end of their third year in the case of females, and a year later in the case of males.

Being subordinate did not prevent individuals from breeding. Females usually gave birth to their first young between the ages of 9 and 12 months, soon after becoming independent of their mothers. However, where densities are high it is known that females have a low success rate in the rearing of their first young (Kean, 1971). Males were observed to mate with females who had not been accompanied by a consort male (e.g. Male 22 and Male 33 with Eve. Ch. 5.214). Also in the absence of an older higher status male, young subordinate males may act as a primary consort male (Ch. 5.212).

In both males and females there was a dominance hierarchy of the absolute ranking type correlated with age and/or size (Ch. 5.33 and 5.4). In the case of females however, daughters sometimes became dominant to their mothers. Alpha individuals were more or less evenly dispersed with at least some degree of exclusive areas, and formed a relatively stable system. Subordinates, especially the younger ones, ranged more widely and therefore were involved in many hierarchies.

Frequency of encounters between individuals of the same sex, particularly females, was low compared with those between different sexes. Many male encounters took place in the vicinity of an oestrous female who acted as a focus of attention for the males. It is suggested that this low frequency is partly the result of mutual avoidance between co-dominants, and of avoidance of a dominant individual by a subordinate. It is also suggested that the dominance relationship is established during initial encounters and maintained by individual recognition with the occasional reinforcement through subsequent encounters.

Olfactory communication with scent marking, serving as individual recognition, is considered to be one of the principal ways by which avoidance is achieved. Individuals, particularly males, marked objects by chinning and chesting or with urine as they travelled within their home ranges. These activities were distributed throughout the home range but were concentrated at den trees and in the vicinity of an oestrous female (Ch. 4.2311). As a result possums were more likely to encounter a fresh scent mark in an area more frequently visited by the scentmarker, and particularly at den trees or in the vicinity of female accompanied by a consort male. Depending on the relative dominance of the individual identified from the scent, the freshness of the scent, and the context, the animal would respond appropriately (e.g. avoidance, the seeking of an aggressive encounter, etc.). The avoidance of an area frequently marked by another individual of the same dominance status would lead to the establishment of exclusive areas. The size of an exclusive area and the frequency with

which it was violated may depend on such factors as the distribution of dens, concentrations of food, and population density.

Auditory communication over a distance is possible. The possum has a unique dilated thyroid cartilage which may act as a resonator (App. III), and the calls are dispersive rather than cohesive. For example several calls are loud, carrying over distances of 200 to 300 m, and consist of two graded series of agonistic calls (the hiss-screech series and the grunt-growl-chatter series) (Ch. 4.144). Most of these calls were not directed at a distant individual but were given in face-to-face interactions (Ch. 4.156). The only exceptions were the short and long chatters, the first of which might have originated in threat and functioned as an alarm call (Ch. 4.1553). The function of the long chatter was unknown. In a face-to-face agonistic interaction the loudness of a call may enhance its effectiveness as a threat and be the primary advantage. The secondary advantage is that such loud calls no doubt convey information to other possums in the vicinity about the source and possibly the type of interaction occurring. Since most agonistic vocalisations are given during courtship (Ch. 5.2114) the locality of a consort pair will be known to neighbouring individuals. This will be an advantage to the consort male because other males will recognise the presence of the consort male and avoid him if he is known to be dominant or co-dominant. Conversely the agonistic calls given during an aggressive mating (without a consort male) may attract males and so ensure multiple copulation with the female which may increase the probability of fertilisation. A loud alarm chatter was often given following an alarm dash and climbing a tree, and other possums sometimes responded in a like manner (Ch. 4.1552). It is possible that ground predators may have been an important selective agent in the development of the chatter as an alarm call.

The female maintained a minimum individual distance of 1 m with the male by means of aggression. To mate, the male had to overcome the aggression of the female. The usual way was for the male to establish a

consort relationship of 30 to 40 days prior to mating. His courtship behaviour, which included appeasement calls (Ch. 5.2114), apparently eliminated the female's aggression during mating (Ch. 5.2113). The consort relationship reduced the risk of injury through fighting and also established the male's claim to the female thus increasing the probability of successful mating by him. It is possible that the female's aggression is reduced at oestrus by hormonal changes, but without a consort male the mating always involved aggression. During such matings the male, by virtue of his slightly larger size, could overcome the female's aggression.

Pair formation was limited to the consort period and did not extend beyond mating, and the same consort pairs were established in successive years if they lived in the same area (e.g. Alec and Alice, Ch. 4.214). At Moggill Farm den sharing between males and females was limited to the consort period (Ch. 5.2113). In different circumstances social attraction in den sharing at other times was indicated by a male and a female kept together in a large cage at Tyne Street. They regularly spent the day huddled together on one shelf although a second similar shelf was available. In New Zealand, where population densities are higher, den sharing is relatively common (Crawley 1973, Pracy and Kean 1969).

Following the joey's emergence from the pouch at the age of 4½ to 5 months, the mother-joey bond was exhibited by a variety of cohesive behaviour. This included allogrooming, nose-to-nose sniffing, "suckling", and "touching". The young possum possessed four distress calls to which the mother responded, particularly when her offspring took part in an agonistic interaction with an adult male. Such cohesive behaviour would appear to favour the formation of at least a mother-offspring family unit. However, such behaviour was not strongly developed and began to disappear with the onset of female aggression when her joey was about nine months old. Only at the den was the young tolerated until it was about

16 months old. The cohesive behaviour during this period was mostly limited to "touching". A juvenile was therefore encouraged to act independently and explore its surroundings whilst still using the security of the maternal den.

Juveniles, when finally evicted from the maternal den, would initially use low quality (generally small) dens in the maternal home range, which were rarely used by adults. The use of these dens gave the juvenile an opportunity to further explore its surroundings and seek a home range of its own. Young males then went through a dispersal phase to establish a home range away from their maternal area, whereas young females usually established a home range in the immediate vicinity of the maternal home range.

To summarise, the dispersion pattern of the brush-tail possum fits the general model of overlapping home ranges with indefensible boundaries, a characteristic found in many mammals (Leyhausen 1965). The defence of dens is consistent with the model proposed by Brown (1964) in which the time and energy spent in the defence of an area is of selective value only for resources for which there is competition and are defensible. The well structured hierarchical system provides a mechanism of differentially eliminating individuals when resources become limiting. In Fisler's (1969) classification of mammalian organisational systems the brush-tail possum has an organisational system based on individuals (I), with a shifting nidic territory (IB2), core monopolisation which may have the occasional conspecific intrusion (IE1), and with a linear type hierarchy (IG1).

7.2 The adaptive significance of the social organisation in arboreal marsupials

The social organisation of a species is considered to be influenced by its environment, and it is probable that in similar environments mammals will have similar selection pressures on the social patterns they develop.

FAMILY	SPECIES	SIZE	HABITAT				ZONE			DIET							ACTIVITY		SHELTER			LITTER	SOCIAL HABIT
		Head-body length (mm)	Closed forest	Open forest	Woodland	Shrubland + Heathland	Terrestrial	Scansorial	Volant	Small verts	Invertebrates	Nectar	Flowers	Fruit	Leaves	Kino	Nocturnal	Diurnal	Existing hollow	Builds nest	None	Teat number	
Macropodidae	Dendrolagus lumholtzi	660	X	.	.	.	X	X	.	.	.	.	.	X	X	.	X	+	.	.	X	?	Post mating pair ?
	Dendrolagus bennettianus	ca."	X	.	.	.	X	X	.	.	.	.	.	X	X	.	X	+	.	.	X	?	" ?
Phascolarctidae	Phascolarctos cinereus	813	.	X	X	.	.	X	.	.	.	.	.	.	X	.	X	.	.	.	X	2	Harem ? (Walker 1964)
	Trichosurus vulpecula*	460	X	X	X	.	X	X	.	.	.	.	X	X	X	.	X	.	X	.	.	2	No post mating pair
Phalangeridae	Trichosurus caninus	ca."	X	.	.	.	X	X	.	.	.	.	X	X	X	.	X	.	X	.	.	2	? (solitary)
	Phalanger maculatus	660	X	.	.	.	.	X	.	X	.	.	X	X	X	.	X	.	?	.	?	4	? (solitary)
	Phalanger orientalis	ca."	X	.	.	.	.	X	.	X	.	.	X	X	X	.	X	.	?	.	?	4	? (solitary)
	Wyulda squamicaudata	.355	+R	+R	.	.	X	X	.	.	X	.	?	X	X	.	X	.	+R?	.	.	?	? (solitary)
Petauridae	Pseudocheirus peregrinus	410	X	X	.	.	.	X	.	.	.	.	X	X	X	.	X	.	.	X	.	4	Post mating pair
	Pseudocheirus herbertensis	ca."	X	.	.	.	.	X	.	.	.	.	?	X	X	.	X	.	.	?	?	4	? (solitary)
	Pseudocheirus archeri	ca."	X	.	.	.	.	X	.	.	.	.	?	X	X	.	X	+	.	?	?	4	? (solitary)
	Hemibelideus lemuroides	ca."	X	.	.	.	.	X	.	.	.	.	?	X	X	.	X	.	.	X	.	?	Post mating pair ?
	Petropseudes dahli	450	.	+R	.	.	X	X	.	.	.	.	X	X	X	.	X	.	+R	.	.	?	Post mating pair ?
	Dactylopsila trivirgata	305	X	.	.	.	.	X	.	.	X	.	.	X	.	.	X	.	X	.	.	?	? (solitary)
	Gymnobelideus leadbeateri	150	.	X	.	.	.	X	.	.	X	?	?	.	.	.	X	.	X	.	.	4	?
	Schoinobates volans	430	.	X	X	.	.	X	X	.	.	.	.	.	X	.	X	.	X	.	.	2	No post mating pair
	Petaurus australis	305	.	X	X	.	.	X	X	.	?	.	?	X	X	X	X	+	X	.	.	?	Post mating pair probable
	Petaurus norfolcensis	250	.	X	X	.	.	X	X	X	X	X	X	X	.	?	X	.	X	.	.	?	Resting pair
	Petaurus breviceps	203	X	X	X	.	.	X	X	.	X	X	X	X	.	?		.	X	.	.	4	Resting family group
Burramyidae	Acrobates pygmaeus	80	.	X	X	.	.	X	X	.	X	X	X	.	.	.	X	.	X	.	.	4	Resting family group
	Cercartetus caudatus	ca.110	X	.	.	.	.	X	.	.	X	.	?	?	.	.	X	.	.	X	.	4	Resting group (sexes seggregated)
	Cercartetus concinnus	75	.	+S	+S	X	X	X	.	.	X	X	X	.	.	.	X	.	X	X	.	6	?
	Cercartetus nanus	106	.	+S	+S	X	.	X	.	.	X	X	X	.	.	.	X	.	?	?	.	4	?
	Cercartetus lepidus	120	.	+S	+S	X	.	X	.	.	X	X	X	.	.	.	X	.	?	?	.	4	?
	Burramys parvus	ca."	.	.	+R	+R	X	.	.	.	X	.	.	X	.	.	X	.	+R?	.	.	4	?
Tarsipedidae	Tarsipes spenserae	76	.	.	+S	X	.	X	.	.	.	X	.	.	.	.	X	.	?	?	.	4	?

*Includes T.arnhemensis

Table 7.1

Relative development of social behaviour and related adaptations in the Australian arboreal marsupials. X = character present; ? = character possibly present; +R = with rocks ; +S = with shrubs. Compiled from Jones 1924; Fleay 1942; Marlow 1962; Troughton 1962; Walker 1964; Winter 1966; Smith R.F.C. 1969; Tyndale-Biscoe 1969; Breeden and Breeden 1970; Ride 1970; Wakefield 1970; Calaby, Dimpel, and McTaggart Cowan 1971; Dimpel and Calaby 1972; Dwyer pers. comm.

This concept has been studied most intensively in the primates. Crook and Gartlan (1966) proposed a series of five "Grades" representing "levels" of adaptation to progressively more open habitats. The concept has been further developed for primates (e.g. Crook 1970, Struhsaker 1969, Eisenberg et al. 1972), and applied to African bovids (Estes 1974 quoted in Kaufmann 1974) and macropod marsupials (Kaufmann 1974) in which similar trends to the primates were observed.

The social organisation is also influenced by phylogenetic relationships (e.g. Struhsaker 1969), so that even closely related species under similar ecological selection pressures retain a basic species pattern (see Nagel 1971, Kummer 1971). Conversely the species pattern may vary within limits for different habitats (see Rowell 1966, Eisenberg et al. 1972).

Marsupials have a number of basic differences from placentals which may result in different social patterns for the two groups. Most obvious is the method of reproduction with the pouch life stage of the young. Other differences are the lower metabolic rate (Dawson and Hulbert 1969), and the lack of corpus callosum in the brain (Matthews 1969, p. 193). There is also a general agreement that marsupials are poorer learners than placentals (Ewer 1968a, p. 355). Kaufmann (1974) considers that the peak of social development in marsupials is lower than in the ungulates, which they parallel in many ways. He studied the whiptail wallaby (one of the more gregarious macropods) and found that cohesion, co-ordination, co-operation, and leadership were all less well developed than in bovids.

Trichosurus vulpecula is a member of Phalangeridae which is one of five families collectively known as phalangerids, among Australian marsupials (Kirsch 1968). The Australian members of this group, and other arboreal marsupials, are listed in Table 7.1 together with information considered relevant to the social organisation of the species (the New Guinea species are omitted). The group is primarily an arboreal one, with some terrestrial (Burramys parvus), or semiterrestrial species

(Trichosurus, Cercartetus concinnus, Wyulda squamicauda, and Petropseudes dahli). The group is also primarily a nocturnal one with only one species (Pseudocheirus archeri) reported to feed during the day also with any regularity (Breeden and Breeden 1970). Petaurus australis has once been reported as feeding during the day (Sault and Taylor 1974), but again it is mainly a nocturnal animal.

Most of the open forest species either use existing hollows (Trichosurus vulpecula and all the gliders) or build a nest (Pseudocheirus peregrinus) for a day roost. The only exception is the koala (Phascolarctos cinereus) which spends the day in an exposed branch crotch. It is also the largest of the open forest species. Of the den users there is a general inverse correlation between the size of the animal and the degree of sociality (Table 7.1). Trichosurus vulpecula is the largest and exhibits little den sharing between adults and is generally a solitary species. The largest of the gliders (Schoinobates volans), which is in the same size range as Trichosurus vulpecula, is thought to be also solitary with pairing restricted to one month (Smith R.F.C. 1969). It is a leaf eater (Marples 1973) and lacks loud vocalisations (Wakefield 1970). The noticeably smaller Petaurus australis may spend the day in small family groups of male, female and juvenile (Fleay 1947), and has loud gliding calls (Wakefield 1970), suggesting that individuals (possibly pairs) keep together at night. Petaurus breviceps which is smaller still has been recorded in groups of up to 12 in one den (Fleay 1947), and has a complex olfactory communication system which includes marking of conspecifics (Schultze-Westrum 1965). The smallest of the gliders, Acrobates pygmaeus may also occur in family groups in the den, and large aggregates are reported (Fleay 1947, p. 97).

It is hypothesised that the size of dens available in trees of the Australian open forest impose limits on the number of individuals that can share a den. For species the size of Trichosurus vulpecula and

Schoinobates volans the limit is one adult plus one juvenile. These two species have the maximum body size concomittent with the use of preexisting arboreal dens. The female is more vulnerable than the male because of the demands made by the growing juvenile. These demands are not just physiological but also physical. A female carrying a juvenile requires additional space in the den as the juvenile increases in size, and she is more prone to falls when carrying a juvenile on her back. It is to her advantage therefore if she controls the use of dens. Not only can she have access to the best dens, but she can also avoid the necessity of moving to another den at dawn. The female's dominance over the male serves this purpose.

Tyndale-Biscoe and Smith (1969) found a significant disparity in the sex ratio of Schoinobates volans with 61% females, owing to differential mortality of juveniles. The number of females breeding each year corresponded to the number of males, with a surplus of non-breeding females. Only one young was raised each year. This is very different from Trichosurus vulpecula where the sex ratio was 1:1 and even females unaccompanied by a consort male bred. Tyndale-Biscoe and Smith (1969) were unable to offer a behavioural mechanism for the social system of Schoinobates, and suggested that it is a mechanism of population control operating in a density-dependent manner on the mortality of male juveniels.

There are at least two possible behavioural explanations for the surplus of non-breeding females in Schoinobates volans. One is that a strong pair bond is established and maintained beyond mating, with the male taking no sexual interest in other females. This explanation seems unlikely because heterosexual pairing was restricted to one month (Smith, R.F.C. 1969). It will be interesting to know if this species does not share dens. The other, and more likely explanation, is that in order to mate a consort period is obligatory. A female glider carrying a large juvenile is likely to be more prone to falls than a deliberate climber like Trichosurus vulpecula, and it is known that Schoinobates does leave

its young in the den (Fleay 1947, and personal observation). Therefore it may be predicted that the selection pressures for female control of dens is greater in Schoinobates volans than in Trichosurus vulpecula and thus produces more aggressive females in the glider. More aggressive females may dispel males as well as other females from dens, and general dominance of females over males, if it exists, would lead to the disparity in the sex ratio. This explanation also serves to interpret a function of an obligatory consort relationship for successful mating. Reduced amount of fighting as a result of consort behaviour would prevent an injury such as one inflicted on the eye which would be more serious to a glider. Surplus females do not mate because of the restricted breeding season which prevents males forming a second consort pair.

Pseudocheirus peregrinus, which belongs to a genus of primarily rain forest species (Table 7.1), has also managed to colonise the open forest. It is primarily a nest builder although it will use hollow limbs. It is in the same size range as Trichosurus vulpecula and Schoinobates volans, but is not so solitary. In one study (Thomson and Owen 1964) nest sharing between males and females was 31.7% and both sexes were observed to build nests. Marsh (1967) reported that the male may stay with the female during the raising of the litter of two, and may even carry the young to safety. Because it is a nest builder the selection pressures for solitariness imposed by the den using habit of the other two open forest phalangerids of equal size do not apply. The assumption is that nest size can be varied to hold a family unit.

The largest of the open forest arboreal marsupials (Phascolarctos cinereus) does not use a den. Although previously considered to be a member of the phalangerid group it probably has closer phylogenetic affinities to the terrestrial wombats of the family Vombatidae (Kirsch 1968). Its size, which apparently permitted it to live without a day time shelter, may have been a preadaptation made during a terrestrial phase of

its evolution. Published accounts of the behaviour of Phascolarctos are still anecdotal. Nevertheless statements that males defend a harem of females (Walker 1964), suggest that Phascolarctos is not as solitary as Trichosurus vulpecula or Schoinobates volans. This may be predicted because the size of a group is not constrained by the size of a den. Because of its closer affinities with the Vombatidae than with any of the phalangerid families, Phascolarctos can be expected to show different behaviour yet it is consistent with the above explanation.

The evidence obtained in New Zealand for den sharing (Pracy and Kean 1969, Crawley 1973), suggests a less solitary mode of life of Trichosurus vulpecula there than at Moggill Farm. In New Zealand the selection pressure on the sole use of a den may not be as great, because much of the habitat is closed forest. It is suggested that the variation, with limits imposed by the genotype, of the social organisation of Trichosurus vulpecula may range from the solitary condition observed at Moggill Farm to a more group type organisation observed in New Zealand. It is not evident how close such a group organisation comes to a family unit as observed in Pseudocheirus peregrinus. Following this reasoning it may be predicted that the closed forest sub-species (johnstoni) of Trichosurus vulpecula and Trichosurus caninus are less solitary.

The arboreal marsupials of the closed forest have 4 to 6 teats, except in the case of Trichosurus caninus (2 teats), whereas the open forest species have 2 except the smallest species (Petaurus breviceps and Acrobates pygmaeus). The smaller potential litter size of open forest species is considered to be a function of the reduced cover. For example, the large bodied Phalanger, the two Australian species of which live in closed forest, have 4 teats compared with the 2 teats in similar sized Trichosurus vulpecula. Trichosurus caninus whilst a closed forest species also lives in fringing open forest and may in fact be a secondary closed forest species evolved from an open forest genus. Similarly the large open forest glider Schoinobates volans and probably Petaurus

australis have 2 teats whereas the same size closed forest species of the family Petauridae have 4 teats where known. Pseudocheirus peregrinus though able to inhabit the open forest because of its nest building ability is considered to be primarily a closed forest species. The small family unit of male, female and young is probably the largest foraging group of closed forest species, exhibited by Hemibelideus lemuroides (Breeden and Breeden 1970, and personal observations), Pseudocheirus peregrinus, and the arboreal macoropod Dendrolagus. Smaller species may have the largest resting groups e.g. Cercartetus caudatus with 4 adult males and 1 juvenile female recorded in one nest (P.D. Dwyer, pers. comm.). Petaurus breviceps is considered to be primarily an open forest species.

Ecological parallels to the phalangerids are to be found in the Old World lemuroids which have a number of nocturnal as well as diurnal species. Following the model developed by Crook and Gartlan (1966) for primates, showing correlates of social organisation with ecology, and subsequently used for bovids by Estes (1974), and for macropod marsupials by Kaufmann (1974), comparisons of social organisation between the phalangerids and the lemuroides may be of interest. Trends in the social organisation of lemurs are correlated with activity rhythm (nocturnal species are less likely to exhibit social groups than diurnal species), diet (insectivorous species are less likely to exhibit social groups than herbivorous species), and for diurnal species cover is important (those species that move into open areas are more likely to exhibit larger groupings) (Martin 1972). Phalangerids are all nocturnal, which is probably an ancestral phylogenetic feature rather than having ecological significance today. Two nocturnal arboreal lemuroides studies (Microcebus murinus, Martin 1972, and Gelago demidovii, Charles-Dominique 1972) both exhibit a tendency to form population nuclei in which females nest in large groups, with males segregated, and with a class of peripheral

males kept outside the nuclei. This type of organisation represents a different social system from that described for Trichosurus vulpecula. However, Cercartetus caudatus, which is similar to Microcebus murinus because it is a small, closed forest, nest building, insectivorous species, may exhibit some form of sex segregation in the nests (P.D. Dwyer, pers. comm.). Until more is known about the closed forest species of phalangerids, it is not evident whether the Microcebus/Gelago pattern is essentially a primate or a more basic mammalian pattern. Closed forest phalangerids possibly show similar trends in their social patterns to the nocturnal lemuroids, but the open forest phalangerids, unlike the nocturnal lemuroides, show social trends clearly related to the use of cover. The brush-tail possum, Trichosurus vulpecula, exemplifies this.

Appendix I

TOOTH WEAR AS AN AGE INDICATOR OF TRICHOSURUS VULPECULA

Tooth wear is one of the few methods that can be used to age adult mammals, and is the only one which can be used on living specimens under field conditions. Tooth wear has been used on a variety of mammals (see Giles 1969) including the Australian Ring-tail Possum (Pseudocheirus peregrinus) (Thomson and Owen 1964).

The technique is subject to two main sources of error. One is the variation in the rate of wear both within and between populations. The other is the misreading of tooth wear classes by the observer.

Geographical differences have been shown for white-tailed deer where the tooth wear criteria for the $7\frac{1}{2}$ year class in New York State fits the $12\frac{1}{2}$ year class in Michigan (Ryel et. al. 1961). Even within the state of Michigan individual variation was sufficient to make it difficult to describe typical wear patterns for $4\frac{1}{2}$ year and older deer (loc. cit.), and for racoons in Illinois individual variation caused a broad overlap for tooth wear classes (Grau et. al. 1970). The range of variation for deer is indicated by Ryel and his co-workers as $\pm$ 1 year for the $3\frac{1}{2}$ year class to a $9\frac{1}{2}$ year old deer being classed as having the wear pattern of a $6\frac{1}{2}$ year old deer. Unfortunately the range of overlap is not given for racoons which have teeth more like those of the brush-tailed possum.

Observational error in the reading of tooth wear may be considerable as demonstrated by Ryel et. al. (1961) when they had 36 observers age 57 jaws of known age deer and obtained a range of error of up to 7 years on the $12\frac{1}{2}$ year jaw. This error can be reduced by defining the wear classes on characters which are either present or absent rather than on characters which grade into one another unless these can be measured accurately (see Robinette et.al. 1957 for molar tooth ratio of mule deer), and by having the ageing done by the same person.

All the examples mentioned above have used dead animals and have used the pattern of tooth wear on more than one tooth. Thomson and Owen (1964)

Figure I.1: Tooth wear classes of the top left molar[1] of *T. vulpecula*.

Exposed dentine shaded. Lingual  Labial

Posterior

Wear Class	Crown of M^1	Description
1		Cusps high and pointed with no apparent wear.
2		Lingual cusps with points worn, but with no dentine exposed.
3		Small crescents of dentine exposed on lingual cusps, but none on labial cusps.
4		Crescents of dentine on lingual cusps larger, but cusps still high and rounded. Dentine exposed on at least 1 labial cusp, but not joined to dentine crescents of lingual cusp.
5	 	Lower limit; dentine of at least 1 labial cusp joined to dentine crescent of lingual cusp. Upper limit; dentine of lingual cusps joined and no longer appear as crescents. Dentine of both labial cusps joined to lingual cusps, but still appear as narrow strips along the cusp ridge.
6	 	Lower limit; lingual cusps flatten -ed and broad band of exposed dentine between the two. Dentine on labial cusps no longer a narrow strip, but a broad band. Upper limit; both lingual and labial cusps flattened with large area of exposed dentine, but still with an enamel indentation between anterior and posterior lingual cusps.
7		Cusps completely obliterated and crown of tooth dished. Enamel indentation between anterior and posterior lingual cusps no longer present.

the wear on the first and second upper molars, using criteria originally devised by Kean for Trichosurus vulpecula but never published.

When attempting to use the technique on living Trichosurus vulpecula in the field it was found extremely difficult to see the wear pattern on the more posterior molars, even on anaesthetised individuals, because of the relatively small gape and wet surface of the tooth. As a result the wear pattern described for Pseudocheirus peregrinus (Thomson and Owen 1964) was modified and used on only the first upper molar, identifying the tooth from the dental formula $I\frac{3}{2}$, $C\frac{1}{0}$, $P\frac{2}{1}$, $M\frac{4}{4}$ given by Jones (1924, p.196).

First the possum was anaesthetised, the pattern of wear drawn on an outline stencil of the tooth crown of the left m^1, and the cusps described as sharp, rounded, flattened, or crown of tooth dished. The equivalent tooth on the opposite jaw was also checked briefly to obtain a criterion of uniform wear.

Tooth wear was divided into classes on the pattern of dentine and pulp exposed (Figure 1.1). Class features vary in their accuracy with a tendency for the lower classes to have more distinct features than the upper classes. The division between class 1 and 2 is one of degree, but in practice the cusps always appeared to be either very sharp or definitely rounded. Class 3 is distinguished from class 2 by the first exposure of dentine on at least one lingual cusp, class 4 is distinguished from class 3 by the first exposure of dentine on at least one labial cusp, and class 5 from class 4 by the first connection between the exposed dentine of at least one lingual and labial cusp. Beyond this point the class features become progressively more blurred, making them rather unsatisfactory.

For many of the possums in the study area two or more readings were made of an individual's tooth wear, some of these readings spanning a time interval of up to 5 years. Ideally the tooth wear classes should be fitted to age by using possums of known age only, but this ideal was only partly realised. Twenty-five individuals of known age (to the nearest month) were available for this and their tooth wear patterns have been set out in the upper half of Figure 1.2. However, with these the oldest possum

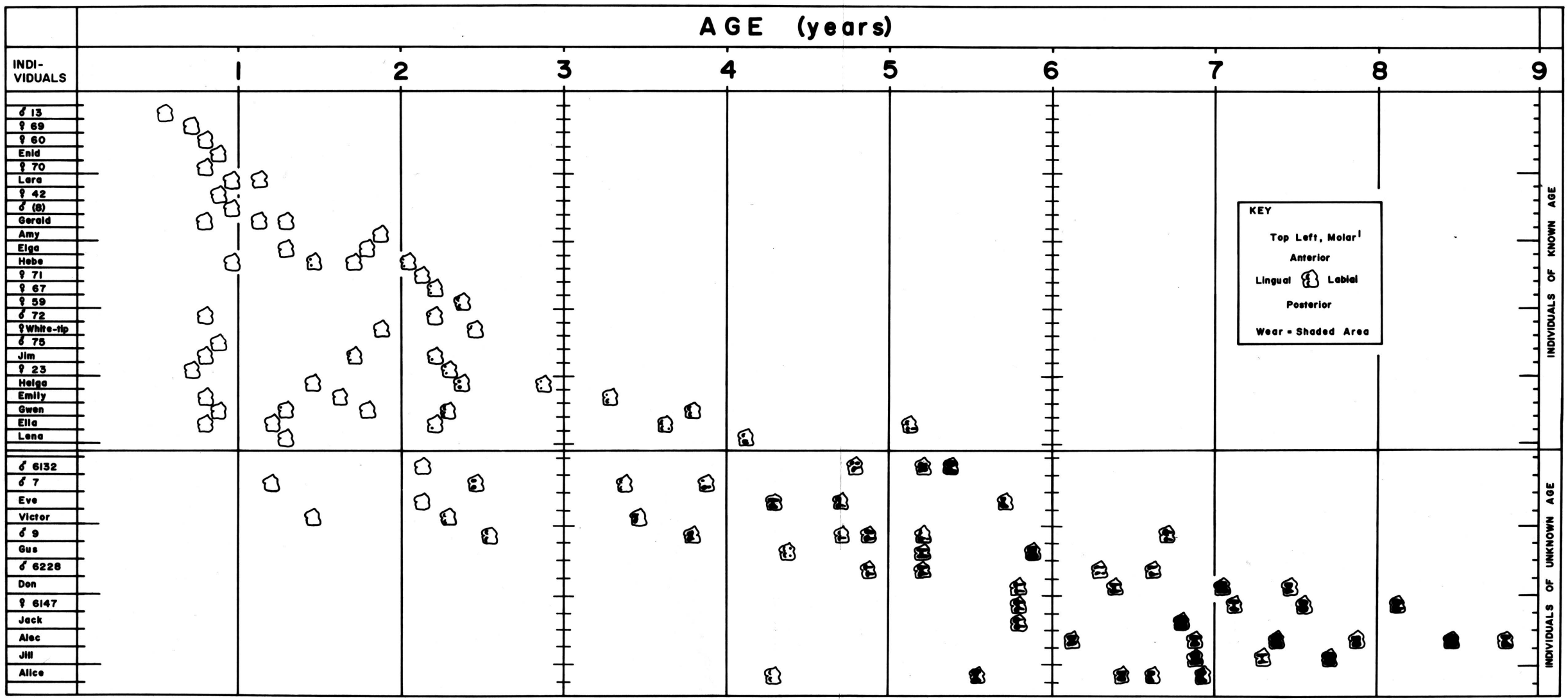


Figure I.2: Crown wear of m^1 as an age indicator in Trichosurus vulpecula. See text for explanation.

(Ella) had reached only class 4 in the tooth wear series.

To complete the relationship between tooth wear and age the tooth wear patterns of a selected number of individuals of unknown age, but with a good chronological span of tooth wear records, have been fitted to the patterns of the known age individuals (see lower half of Figure 1.2). This fitting was done by eye and the patterns positioned according to how they fitted with those of known age individuals. Some of the patterns of unknown age individuals could not be fitted directly to the known age patterns, but had to be fitted to unknown age patterns previously fitted to known age patterns and the error is likely to be greater e.g. Don, Female 6147, Jack, Alec, Jill and Alice.

Table 1.1

Age span of tooth wear classes of T.vulpecula from Moggill Farm.

Tooth wear class	Age span (months)	Degree of reliability - whether based on animals of known or unknown age
1	- 26	
2	16 - 35	Known age
3	28 - 46	
		Lower limit known age
4	44 - 63	
		Upper limit unknown age
5	52 - 81	
6	63 - 106	Unknown age
7	71 -	

The age span for each wear class (Table 1.1) was determined from Figure 1.2. The accuracy of this table becomes progressively less for the higher classes as the determination becomes more and more dependent on possums of unknown age. The upper limit of class 4, and both lower and upper limits for classes 5, 6 and 7 must therefore be considered as only very approximate until they have been checked against animals of known age, or against a more accurate ageing technique such as the deposition of

cementum layers which Pekelharing (1970) has already applied to T.vulpecula, but which requires dead not living animals.

In practice the main difficulty was the actual reading of the tooth in the living animal. Although the first molar is the most anterior of the four-cusped teeth, the tooth still has to be viewed at an awkward angle which often made it difficult to see the wear pattern on the glistening surface of the tooth. This difficulty together with the rather unsatisfactory definitions of wear patterns for the higher classes led to obvious errors in which the wear appeared to regress rather than progress between consecutive readings. For example the readings for Male 9 go 3,3 (poor reading), 5,5,4,5; those for Jill go 6,5,6; and those for Gwen go 1,2,1,3,3. However, most of these errors involved adjacent classes, and they occurred more frequently with the higher classes.

Only one example of uneven tooth wear was detected. This was for Male 6181 whose teeth on each side of the jaw were classed as 2 and 4 respectively.

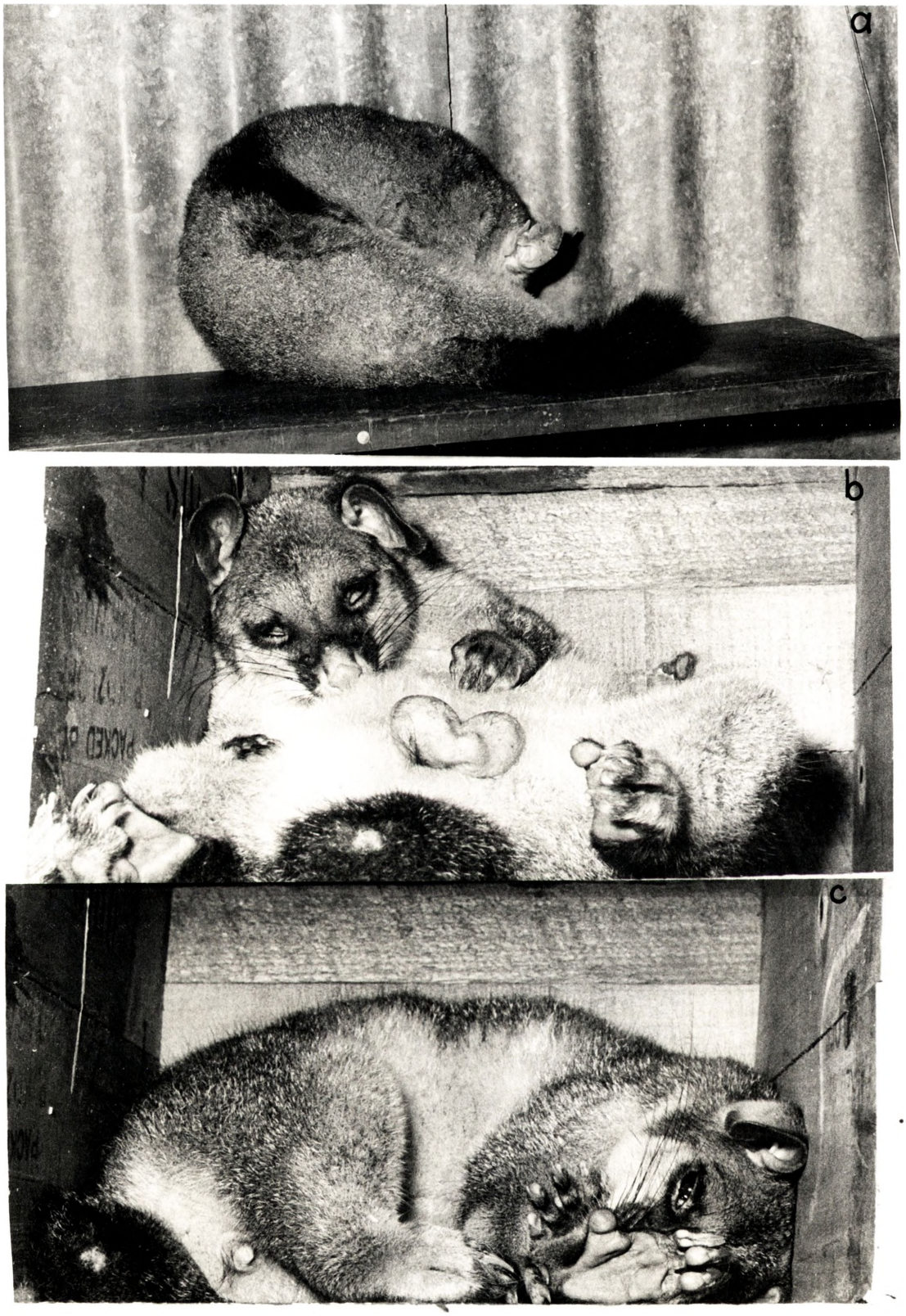


Figure II.1: Sleeping postures a) rump position, when the head is usually tucked more into the abdomen, b) back position, c) side position. b and c are of a tailless male.

Appendix II

INDIVIDUAL BEHAVIOUR

II.1 SLEEPING, RESTING & SITTING POSTURES

Several sleeping postures may be adopted by the possum in its den during the day. Most commonly seen when there is sufficient room, as on the shelves used for the captive possums, is one in which the possum sits back on its haunches with the back legs and tail stretched out in front, and the head and front legs tucked into the abdomen (Fig. II.1a), a posture that can be maintained without leaning against anything. On hot afternoons the possum may sprawl out on its back, with the legs spread to each side, and with the head and tail flat on the floor. If the quarters are cramped the head may be propped against the side of the den with the chin resting on the chest (Fig. II.1b). In a third posture, also used on hot days, the possum lies on its side with the feet bunched together, the nose tucked between the front legs and the tail curled forward (Fig. II.1c). Obviously in cramped dens the sleeping posture may have to be modified. For example in the very narrow den T92 Male 32 was seen sleeping flat on his belly facing the den entrance, his front legs stretched out in front and his chin pressed hard down on his legs by the den roof.

Apart from sleeping in a den during the day a possum may doze in a tree at night. This it does in a crouched position on an horizontal branch, with its head tucked between the front paws, and its tail hanging loosely to one side or rested on the branch behind. A female with a bulging pouch sits upright with her head dropped forward onto her chest and her nose more or less in the opening of the pouch. The most characteristic feature of dozing was the completely relaxed droop of the head and nose tucked between the forepaws, a posture usually adopted by the head slowly dropping, as the possum obviously dozed-off. The eyes were usually closed especially if the posture had been maintained for any length of time.

Resting as opposed to dozing is distinguished by the position of the head which is not tucked between the front legs, but which hangs in a very

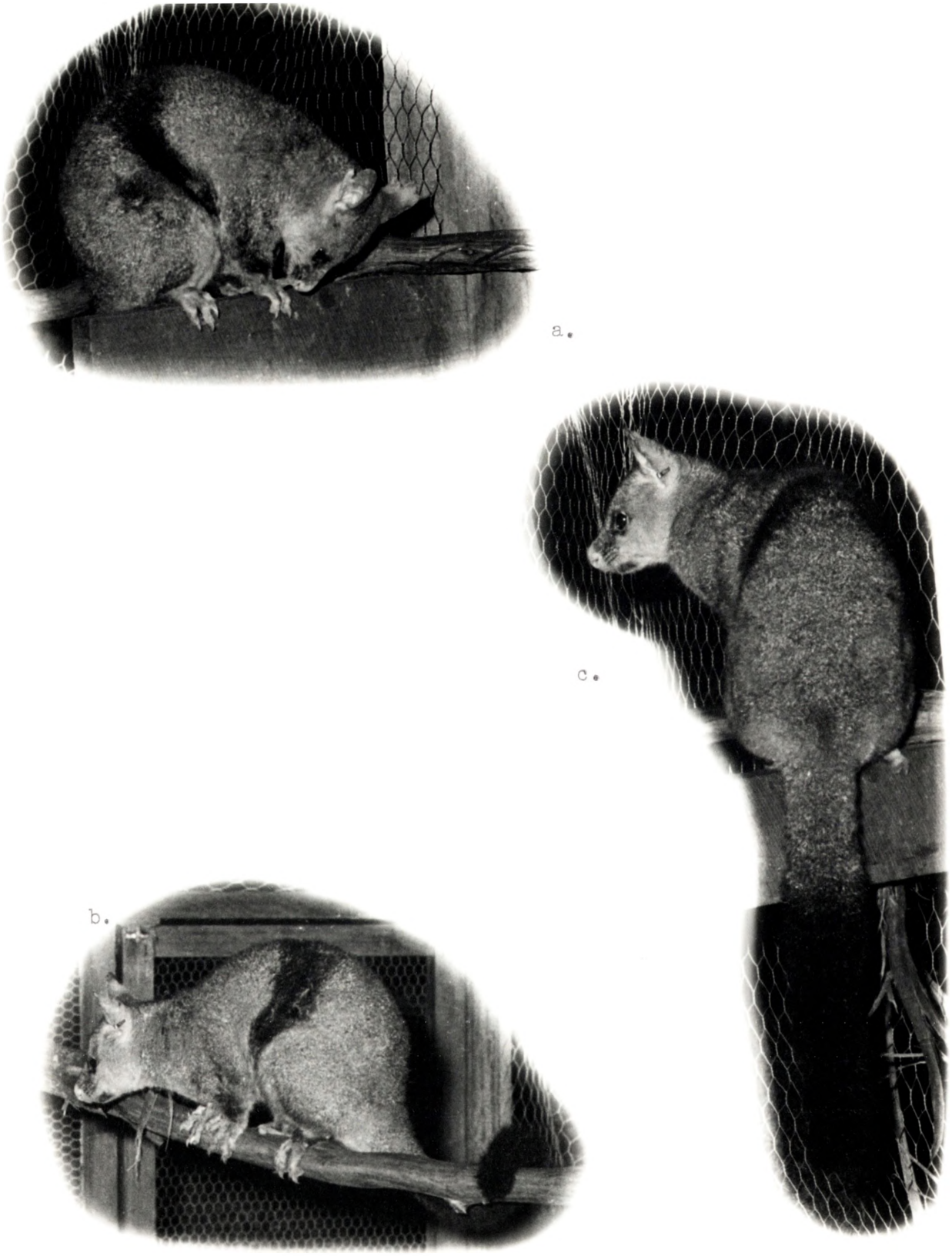


Figure II.2: Resting and sitting postures;
a) resting, note drooping head;
b) crouched sitting;
c) upright sitting.

relaxed manner with the nose pointing directly at the ground (Fig. II.2a), and sometimes hanging below the upper level of the branch. The eyes remain open.

The two most common sitting postures are a crouched position similar to the resting posture, and a more upright one. In the crouched position the head may be held low, but distinguished from the resting position by the nose being held at an oblique angle to the ground, the ears being pricked up, and by the alert look on the face, all of which give the impression of the possum gazing into the night (Fig. II.2b). In the upright posture the feet are held close together, with the front legs straight and the head held high (Fig. II.2c). A common modification of the upright posture occurs when a possum is sitting in a crotch between two branches. It will sit back with its back resting against one branch and either both or one front paw resting on the other branch at shoulder height.

A possum was never seen reclining on a branch in the manner shown by primates and felids.

Stretching was never observed which was surprising considering some of the very cramped dens used.

Yawning was observed only 2 or 3 times.

II.2 LOCOMOTION

The possum is well adapted for climbing with its sharp claws and prehensile tail. All digits except thumb of the hind foot posses sharp non-retractile claws, which enable the five digits of the front foot and the two large digits (4 & 5) of the hind foot to grip the bark of the tree A slightly wider gap between digits 2 and 3 of the front foot enable the possum to grasp a thin branch with two digits to one side and three the other, while the clawless thumb of the hind foot which is held at right angles to the other digits can grip thin branches, appears to improve the gripping power of the hind foot on rough bark, and may help balance when the possum stands bipedally. The long bushy tail is bare on the ventral surface for the distal half, and the last 1-2cm is completely bare giving

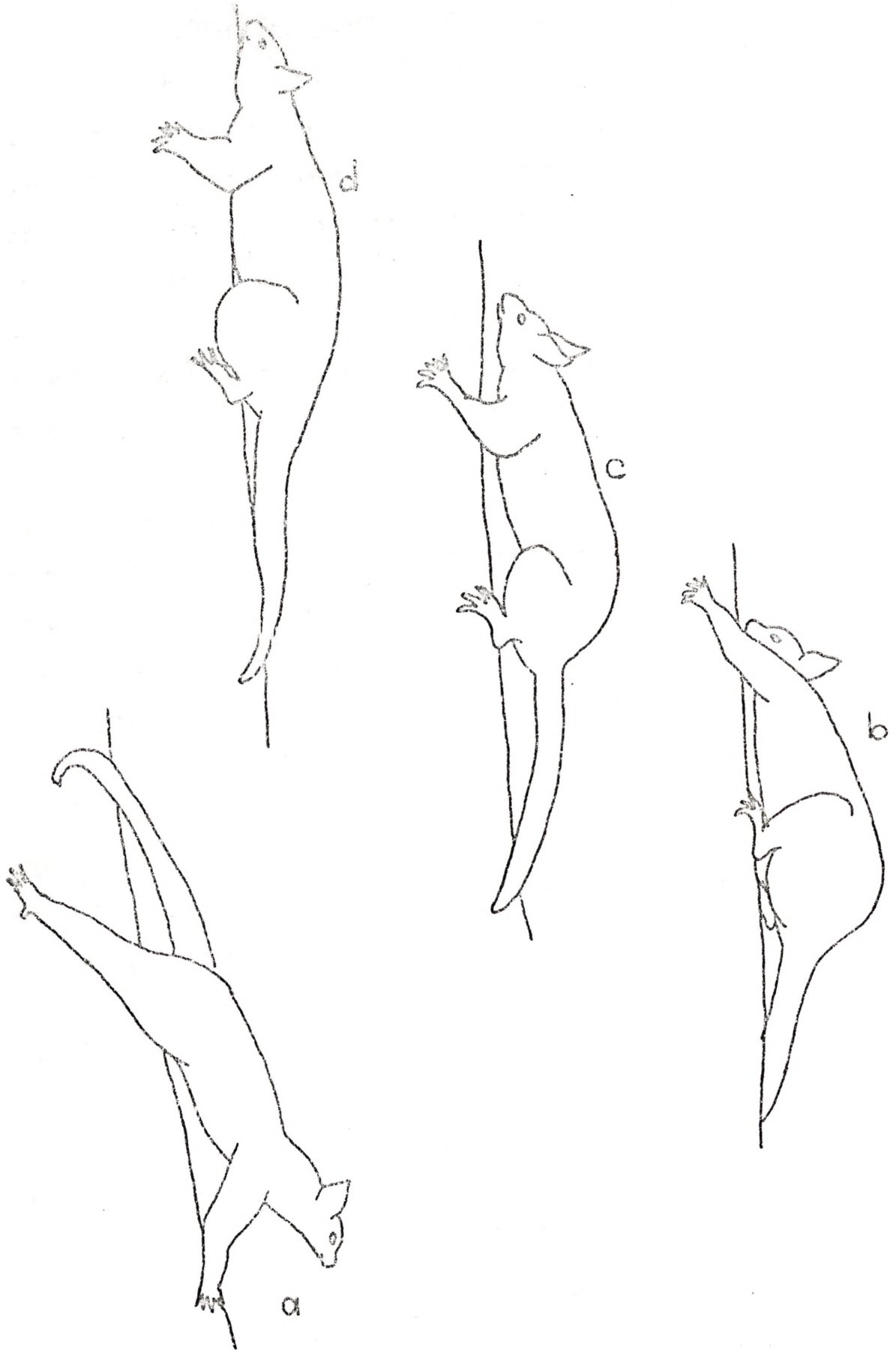


Figure II.3 : Method of descending (a) and ascending (b-d) a vertical tree trunk (a, drawn; b-d traced from photographs).

it the appearance of a nailless finger (Troughton 1962).

A vertical tree trunk is descended in a head down spread eagled manner, the hind feet trailing behind with the claws of the two larger digits gripping the bark and the front legs spread out in front to act as a brace (Fig. II.3a). The hind feet are released alternately and the front feet walk down the trunk, but in a very rapid descent the possums lopes down the trunk with both hind feet being released simultaneously. The tail grips branches or any small projection on the trunk. Although the possum can hang by its tail alone, it rarely does so, more commonly using it as an additional means of gripping a branch.

During its descent a possum will frequently stop to sit on a branch by the trunk as it gazes into the night, usually with a longer pause on the bottom branch before making a fairly rapid descent of the last 4-6m of the trunk. Even on this last stretch of the trunk the possum will sometimes pause in the head down position to look around. Alice once maintained such a head down pause for 10 min and lifted her chest further away from the trunk by bringing her front feet closer together. Rarely does a possum climb right to the base of the tree as it usually jumps to the ground from a height of 0.1 to 1m to land about 1m from the base. The highest such jump made by an undisturbed possum was 2m by a juvenile male. When frightened a possum will leap from heights of up to 6m with legs spread wide apart, like those of a glider, to land with a heavy thud.

The ascent of a vertical trunk is usually by a series of bounds with the hind feet, which are tucked in under the body, providing the thrust and the front feet, held upwards and outwards, gripping the trunk. The hind legs thrust upwards together and at some point in this thrust the front legs are swung rapidly upwards in unison to take a fresh grip on the trunk (Fig. II.3b-d). It looks as though the possum completely releases its hold on the trunk for a brief instance in each bound, but this would have to be checked on film. Another method of climbing was a hand over hand action. This was not often used on a large trunk and then only

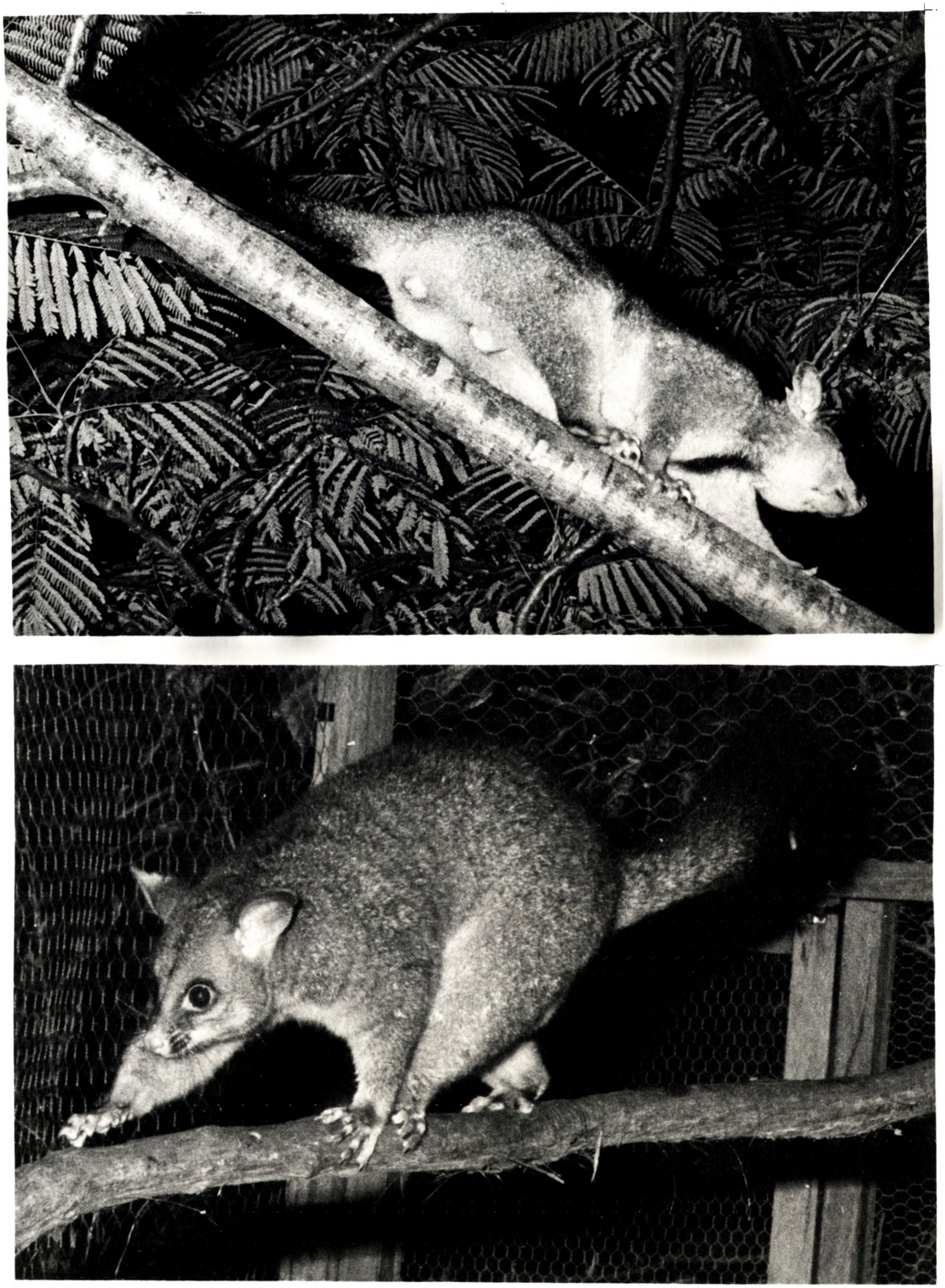


Figure II.4: Walking on; a) sloping branch, note bare skin under prehensile tail which is kept close to the branch, and the dark sternal gland on thorax; b) horizontal branch, note tail held horizontally.

when climbing very slowly, usually while sniffing at the trunk. It was more frequently used on saplings with trunks thin enough for the possum to reach round the back of the trunk with its front paws, but even so it was not a common method of climbing a vertical trunk.

Before climbing a tree a possum usually stops about 0.3m from the base, looks up the tree, then flexes its limbs and leaps onto the trunk 0.3 to 0.5m from the ground. Very occasionally this spring was ommitted and instead the possum walked right up to the tree and climbed onto the base. This is sometimes done after a possum has stood on its hind legs to sniff at the trunk, although even in this situation it was more common for the possum to drop back onto all fours and then to spring onto the trunk.

Once on the trunk a possum may pause briefly before climbing to the lowest limb where it usually stops for a while. The speed of climbing varies from being very rapid, with the animal literally bolting up the tree, to a very slow climb with frequent stops. Females with a large joey in the pouch find climbing particularly awkward. It is obviously very laborious and even hazardous when a joey is riding on her back, and she may stop every 2m or so, apparently to rest.

On branches 40° or more to the vertical the possum uses a typical quadrupedal gait (Fig. II.4). On coming down a steep branch the hind feet are brought forward under the abdomen, with the thumb of the hind foot pointing directly down the branch and the clawed toes at right angles to the body. The walking ascent on a steep thin branch is sometimes accomplished by a hand over hand action with the forepaws reaching round to the back of the branch.

The possum shows a decided preference to ascend by a sloping, even though circuitous route, rather than by a vertical climb which may be more direct but which is obviously more strenuous.

Although the possum is a good climber and even a rapid climber when need be, it is a careful diliberate climber rather than an agile one. Instead of leaping from branch to branch it will cross from one to the

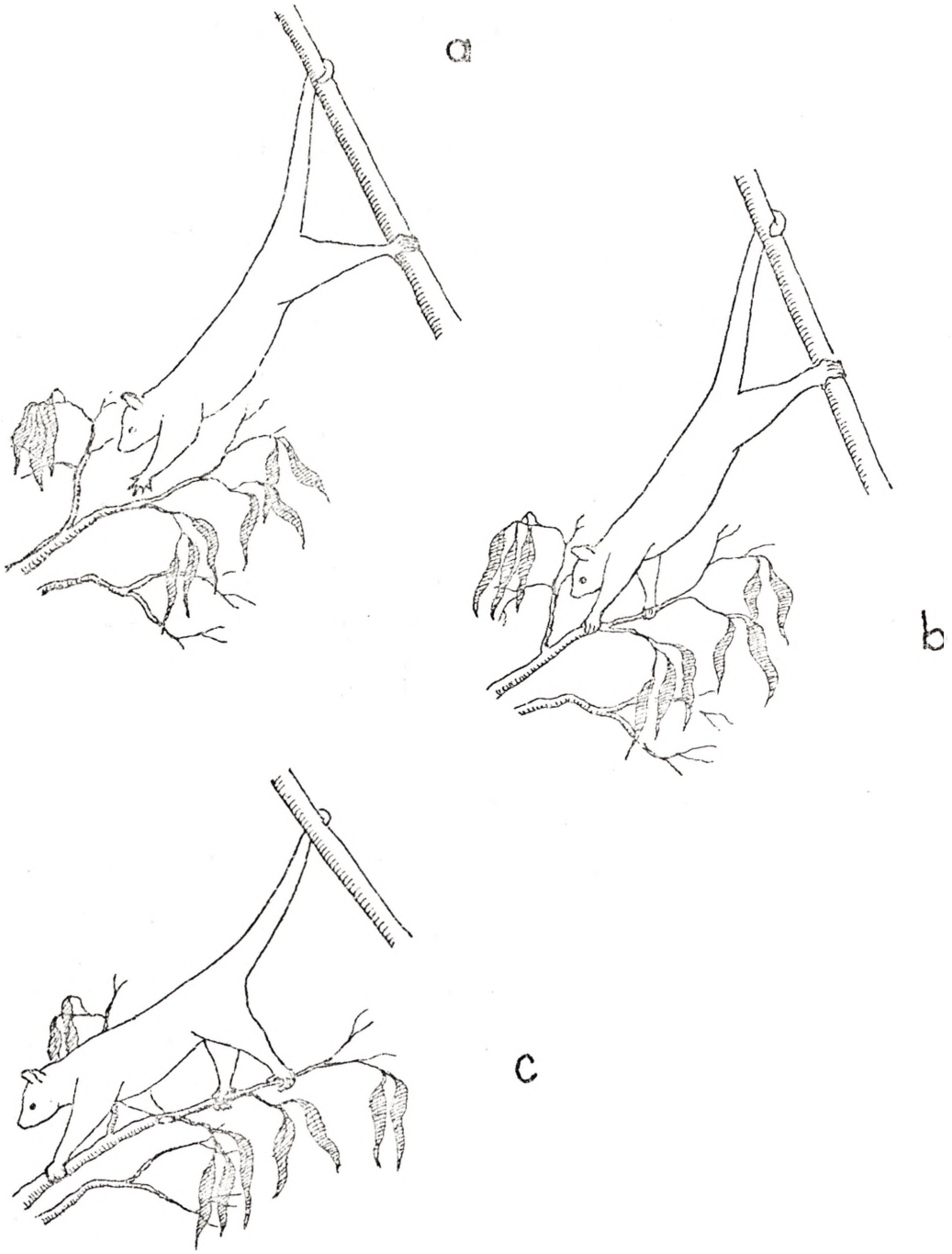


Figure II.5 : Crossing from the canopy of one tree to that of an adjacent tree. a) reaching across, b) pulling in branch hand over hand, c) transfering hind feet. (Drawn by D. Mackenzie)

other by walking back to the trunk then out along the new branch. However, it will make short leaps of about 1m from one firm branch to another firm branch i.e. if the branches are over about 10cm in diameter, or it will jump from a branch across to a vertical trunk even when the latter is a smooth trunk of a gum tree, where it is able to cling with surprising tenacity.

Crossing from the canopy of one tree to that of an adjacent tree is done slowly and carefully and at all times the possum maintains a firm grip on the thin branches. Reaching across to a branch of the adjacent tree may entail hanging by the hind feet and tail while stretching out with the front feet for the next branch (Fig. II.5a). Sometimes the attempts to reach across a gap may be vigorous enough to cause the possum to swing backwards and forwards, and although it will use this swinging to its advantage the possum does not deliberately start swinging before reaching out for a branch. If a possum fails to reach across a gap it may move along the branch to try at other places, but may keep returning to try at the original place. Once a twig or branch of the other tree is grasped, it is pulled in hand over hand (Fig. II.5b) until the hind feet can reach it (Fig. II.5c). Only then will the tail release its grip of the first tree and the complete transfer of weight will often cause the possum to swing violently downwards on the new branch.

Very rarely a possum will jump into the canopy of an adjacent tree or from one very thin branch to another, but only when chased by another possum or, as on one occasion, when a male appeared particularly keen to follow an oestrous female and made a 1-1.5m leap into the thin twigs at the end of a branch. In these leaps the possum usually lands clumsily without catching hold of a preselected twig.

This caution is perhaps justified by a nocturnal animal in the sparse canopy of a eucalypt tree where to miss its footing would usually mean falling to the ground.

Balance seemed to be a minor role of the tail. In three observations the tail appeared to act as a balancing organ by being waved about in an

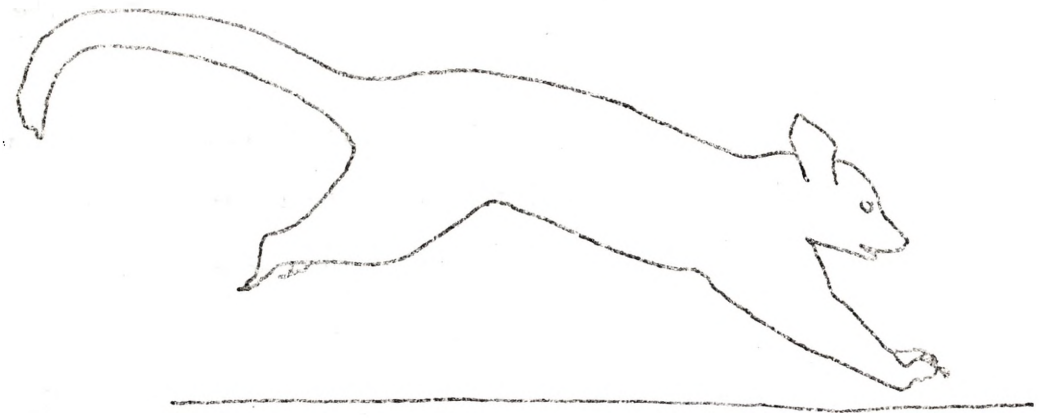


Figure II.6 : Fast bound (traced from photograph).

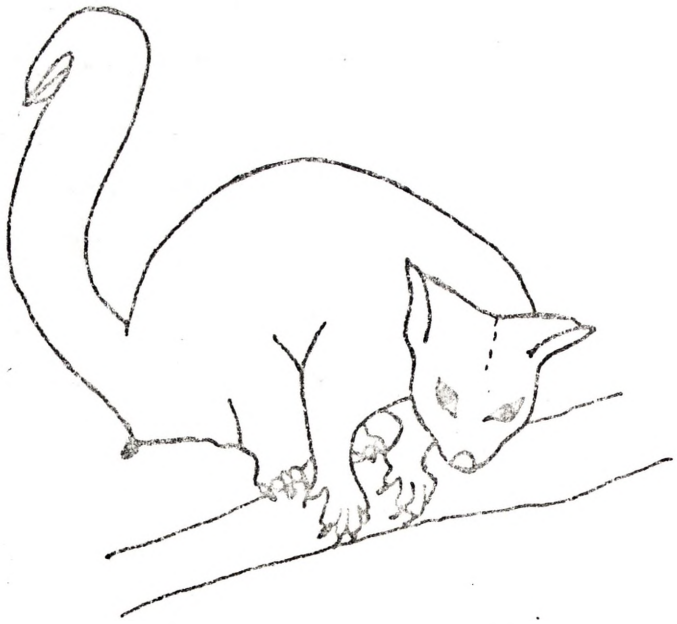


Figure II.7 : Defecating whilst turned transversally to the branch (traced from photograph).

erratic 'propeller' fashion in line with the body, twice by a female with a joey riding on her back and once by an adult male. Usually, however, the balance of a possum, even on the thinnest of branches appeared to be maintained without the aid of the tail and seemed to rely more on the strong grip of the hands and feet.

One other method of progressing along an horizontal branch and which was used to pass another possum sitting on the branch, was to swing under the branch and to climb along it upside down, 'sloth-like', for about 1m before climbing back up onto the branch again beyond the sitting possum. This was twice used by a joey to pass its mother, and occasionally by a juvenile or adult to pass an hostile possum when cornered at the end of a branch.

Although primarily an arboreal animal the possum may spend a considerable part of the night on the ground and can travel rapidly when necessary. The walk is a typical quadrupedal mammalian type, but with a characteristic flat footed waddle. This waddle is imparted by the plantigrade feet, more pronounced in the hind feet, and the wide hind quarters in relation to the forequarters so that the hind feet are held further apart than the front feet and at an angle of about 30° to the long axis. This waddle is particularly pronounced when a female has a large joey in the pouch. The trot is a speeded up version of the walk. The fastest gait is the bound in which the front legs move together and similarly with the hind legs (Fig. II.6). A slow high bound may be used to travel through tall wet grass or over ground cluttered with debris, and in this the tail is held more arched than in the fast bound.

II.3 ELIMINATION

Defecation is often performed by turning transversally to the branch, lowering the head and raising the tail (Fig. II.7) which allows the faeces to drop to the ground. However, the possum may also defecate when walking along a branch without turning transversally, when sitting in a clump of foliage, or when on the ground.

There was no evidence to suggest that faeces were deposited other

than at random. In all 17 observations, defecation occurred away from the den tree, suggesting an avoidance of the den tree. On the other hand possums are notorious for fouling the ceilings of houses used as dens, with both faeces and urine. Nor was there any evidence that faeces were used to scent mark branches, because the individual scats are hard and cylindrical and roll off all but the largest of branches.

Urination is performed in three different ways, as described by Kean (1967). The behaviour of two - the sigmoid strip and the drip trail - suggest that the deposition of the urine has a signal function and are therefore discussed in Chapter 4.

With the third, urine is released as a copious stream or urine cascade. No definite behaviour pattern is associated with the urine cascade and its function appears to be mainly physiological or associated fear. It was observed only twice under natural conditions, once when a female was feeding in a clump of foliage, and once when a male climbed the trunk of a female's den tree to join her. Most observations of the urine cascade occurred when a captured possum had been released. On leaving the trap a possum often paused and urinated before bounding away. Also a captured possum when handled frequently released a copious stream of urine.

II.4 GROOMING

The possum has a soft thick coat of fur and it uses four ways to groom it and other parts of the body.

Face washing is accomplished by licking the inner edge of the wrists then rubbing the wrists forward and downward over the face. Usually only one wrist is used at a time, but sometimes both wrists are used either alternately or together. Jones (1921) describes the palm of the hands being licked prior to face washing, but in the present study palm licking was not observed in this context.

Nibbling of the fur with the teeth is used to groom the flanks, rump, hind legs and belly. Characteristically the possum sits upright with one front leg flung over its rump. It may even grasp the fur with its front paw to help pull itself round to get at awkward places, but the possum never

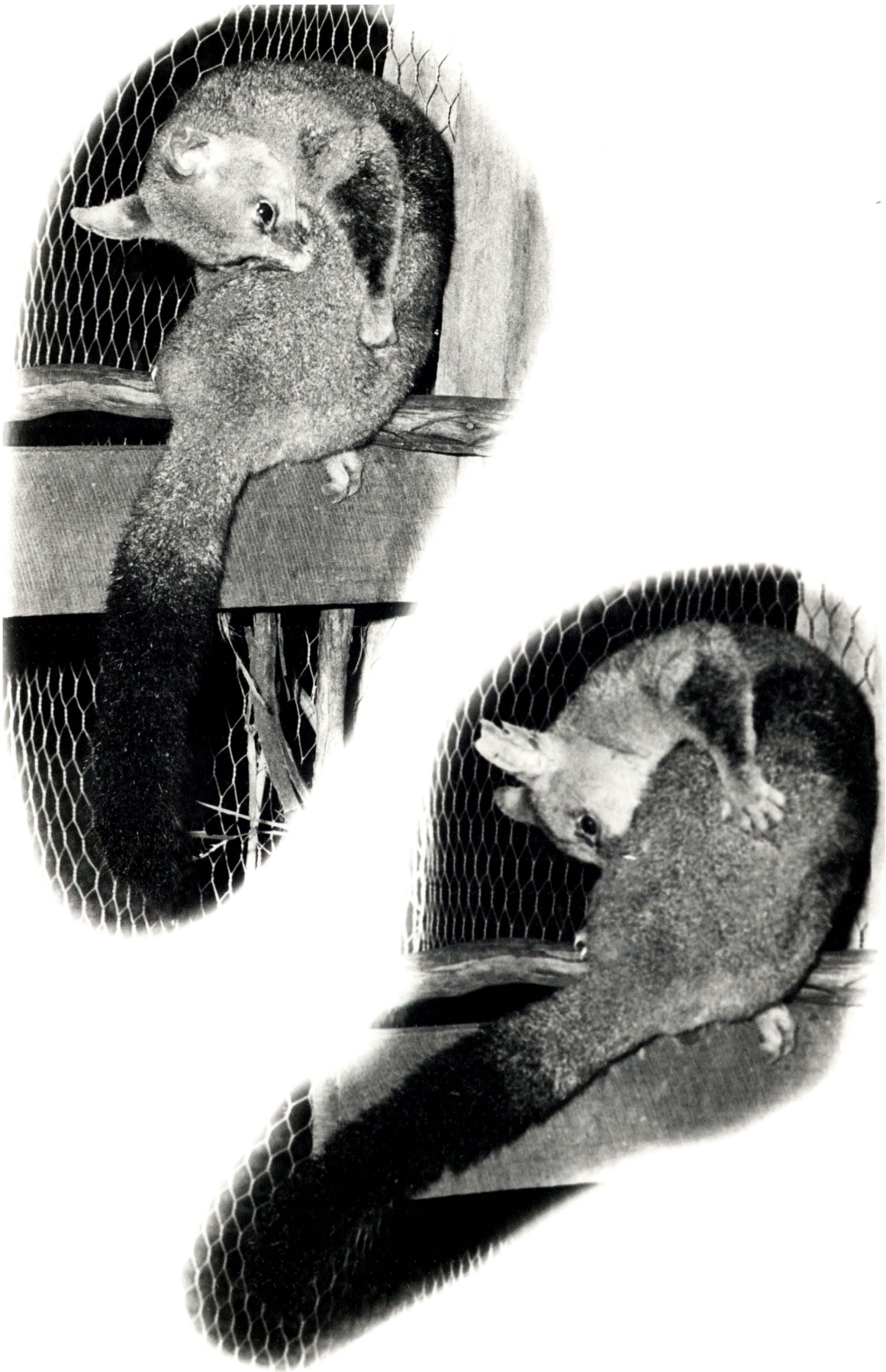


Figure II.8: Grooming - fur nibbling, note fore paw gripping fur in top photograph as the possum grooms the dorso-lateral area of rump.

Figure II.9: Grooming - scratching.
a) back of head and b) side of face.
In both note the position of the syndactyl toes.

Figure II.10 : Licking syndactyl toes of hind foot following scratching by the hind foot (traced from photograph).

Figure II.11 : licking cloacal region (traced from photograph).

uses the front paws to part the fur in the area being groomed (Fig. II.8). The tail is groomed in a similar manner and to get at the more distal parts it is curled forward between the hind legs and held by the front paws.

Scratching was performed by the hind foot. The areas groomed by scratching are the head (mainly behind the ears), shoulders, front legs, chest, belly and the back of the thigh (Fig. II.9). This last area is reached by the possum standing on three legs and scratching the back of the thigh with the other hind leg bent under the tail, and with extremely rapid strokes apparently using the syndactyle toes. Typically scratching consisted of a few very rapid short strokes followed by licking of the hind foot (Fig. II.10). In 20 recorded series of scratching, licking of the hind foot never preceded the scratching, in 5 scratching was not followed by licking, but in the remaining 15 scratching alternated with licking and 14 of these bouts terminated with licking of the hind foot. Licking, therefore, appears to be to clean the foot after it has scratched the fur rather than to prepare the foot in any way for scratching. Jones (1921) considered that the syndactyle toes are adapted as fur combs and states "The hair is raked through by this specialized hair comb, and then the comb is cleansed by the tongue and teeth. Not only is this toilet-use the obvious function of these digits, but it is the only function that they posses, so far as I can learn after hours of watching at all times and seasons". It is extremely difficult to see whether in fact the syndactyl toes are used because the foot is a blur when scratching. No observations were made of slow combing or scratching movements. However, Figure II.11 shows that it is the syndactyl toes which are licked which supports the statement of Jones' that the syndactyl toes are used as a comb. "Alec scratching with both hind and forefoot alternately" is the only record I have of the forefoot being used. Unfortunately the observation was made right at the beginning of the study and was not amplified.

Licking is used to clean the paws, cloaca, pouch and penis. When licking the cloaca (Fig. II.11) or the penis, which becomes semi-erect

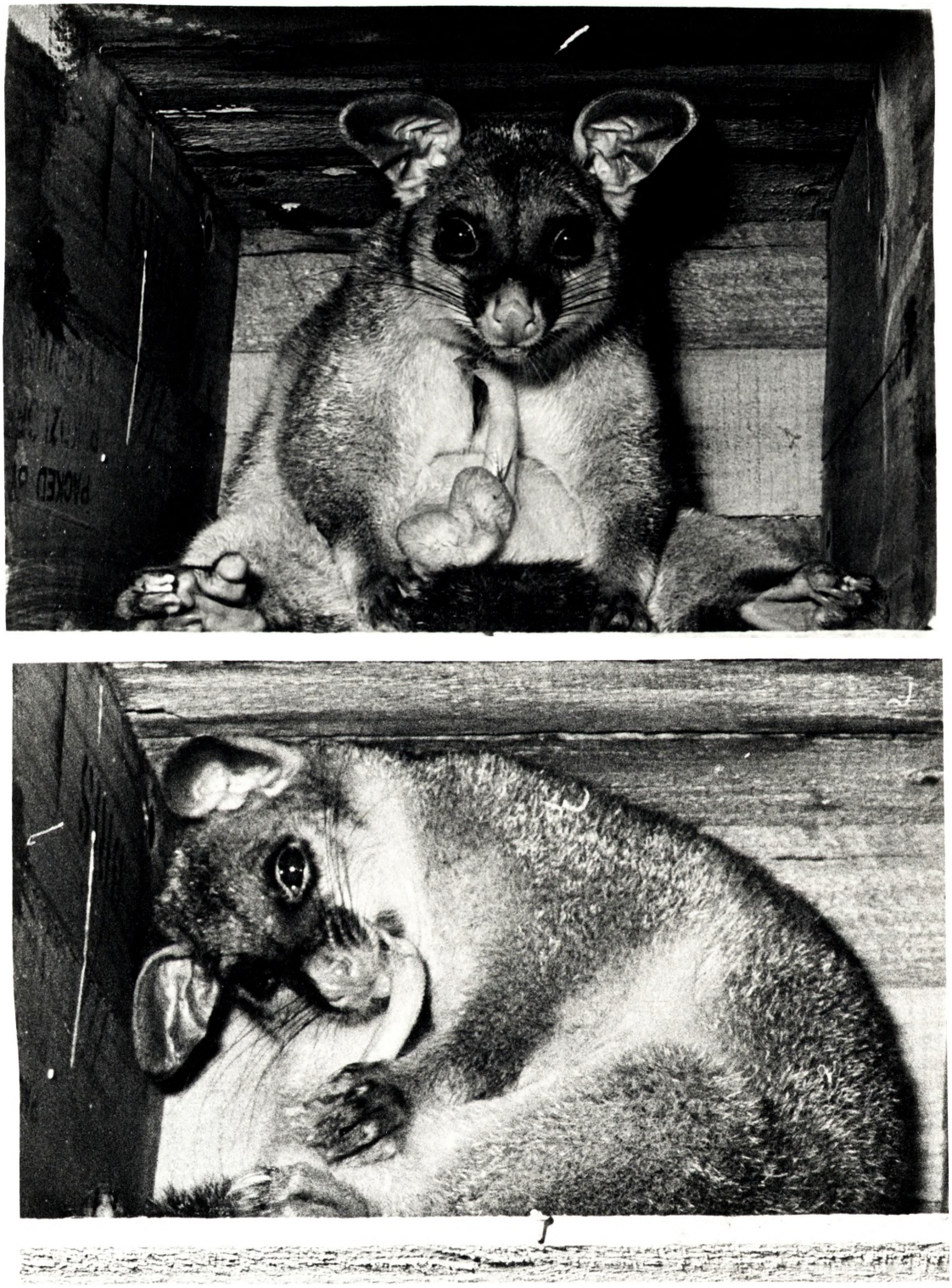


Figure II.12: Grooming - penis licking.
Note semi-erect penis.

(Fig. II.12) the possum sits back on its haunches with one or both hind legs and tail stretched out in front, one front leg steadies the possum, and the other either dangles loosely down its side or grips its thigh. With pouch washing the female typically sits upright with her nose buried in the pouch. Her front paws rest each side of the pouch and once it looked as though she was holding open the pouch with her front paws. Pouch washing was only observed when the female had a fairly large joey in the pouch, so that the pouch bulged out in front of her as she sat upright on a branch. The female does, however, clean the caked wax from the pouch just before the joey is born, but this was never observed. The paw licking described by Jones (1921), in which the possum thoroughly licks the palm of its hand, appears to be to clean the paws themselves and not to wash the face as he claimed. Paw licking can be easily induced by feeding the possum jam or some other sticky food.

Grooming bouts varied in length from very brief ones consisting of one action - "Jill scratched her right arm pit with her right foot" to much longer bouts such as the one given in the following protocol:

> 21.1.69 "19.33.....Female 6147 scratching left flank with left hind foot, licked foot, hind foot down. Now mouth grooming pouch region, mouth grooming dorsal base of tail. She has brought her tail forward and holding it with her left hand as she grooms the tail - the tail is not between her legs. Now mouth grooming the tip of the tail holding it with her left hand. Scratching left flank with left hind foot, licking hind foot which she keeps level with her elbow, scratching back of the thigh. Scratching behind ear with hind foot, licked foot, scratches, licked foot, scratching behind elbow, licking foot, foot down and sitting".

II.5 FEEDING

Feeding occurs both in trees and on the ground and usually involves some manipulation of the food with the front paws. When feeding on leaves the possum will sit or stand on a branch and reach out with one front paw for a leafy branch or a single leaf and pull it towards itself. The possum then continues to hold the leaf by the petiole or the branch very close to the leaf as it takes bites from the blade of the leaf. Typically the petiole, the base of the leaf, and part of the midrib are left uneaten

(see Pracy and Kean 1969). The leaves of Eucalyptus hemipholea are broad and tough and a distinct tearing can be heard 20-30m away, as the possum rips pieces cut of the leaf. With the thinner more delicate leaves of E.crebra and E.terreticornis very little sound is made. When feeding on eucalypt blossum the possum manipulates the branch in a similar way except that it tends to eat the whole flower.

When feeding in mistletoe clumps with their long trailing stems the possum hangs vertically as it feeds. It grips the branch with its hind feet and tail and manipulates the trailing stems with either one or both hands while it nibbles the sessile fruit or flowers (Fig. II.13). Occasionally the possum, particularly young ones, will hang vertically when feeding in foliage other than that of mistletoe.

Figure II.13. Typical posture adopted when feeding on the buds of the mistletoe Amyema miquelii. (Drawn by M. MacKenzie).

On the ground short vegetation was nibbled without any manipulation with the hands, but herbs taller than about 10cm were often grasped, but

never plucked, with one hand as the possum took bites out of the leaves.

Pieces of food, such as apple, bread etc., were first picked up by the mouth then held by one or both front paws as the food was eaten (Fig. II.14a,b), never visa versa. When proffered food by hand a tame possum pulled one's hand closer with a fore paw to take the food in its mouth. The seemingly easier way of taking the offered food in its outstretched paw was not done. The only situation in which food was observed to be picked up by the front paw first occurred when a possum was feeding on dried peas which were completely covered by water (Fig. II.14c

Capture of live prey was once observed, but showed a very rudimentary development of a possum's ability to do so. A tame female carefully sniffed a leaf on the underside of which was a 8cm hawk moth caterpillar. She made a rather hesitant lunging bite at the caterpillar but missed because the caterpillar immediately dropped to the ground. I replaced the caterpillar on the leaf and the process was repeated. On her third try the female made a clumsy 8cm pounce with her front paws but again missed. On her fourth try she made another clumsy pounce and caught the caterpillar before it dropped. She handled it gingerly as though expecting it to bite, but soon pulled its head off with her teeth and ate the whole caterpillar, proceeding from the head to the tail. She held the caterpillar in her hands as she ate it. She obviously recognised it as animal prey from the way she attempted to catch it, an attempt however, that would have been unsuccessful except for my intervention. There is one report of a 'grey possum' - presumably T.vulpecula - killing chickens (Anon 1935) which I was inclined to disbelieve until seeing the above performance with the caterpillar. Under special circumstances a possum amy be able to develop this rudimentary ability to catch live prey, particularly if the prey is a 'captive' prey such as chickens in a coop.

II.6 DRINKING

The presence of free water did not appear to be essential because many home ranges did not contain permanent water and on summer nights dew frequently did not form. However, if free water was present it was utilised.

Dew settled on the ground in open areas away from trees, and on the upper surface of the tree canopy, giving the leaves a silvery sheen. Occasionally a possum licked dew from the grass but more frequently from the leaves in the upper canopy. To reach the dew covered leaves the possum often projected beyond the silhoueted cutline of the canopy and it was this characteristic, together with the silvery sheen of the leaves which, more often than not, was used to determine that a possum was dew licking. In all other respects it was virtually impossible to distinguish it from feeding because it usually took place right at the top of a tree. Rain was also licked from branches and leaves on rare occasions.

Dew licking was confined to the later half of the night, mostly the early morning, and from March to November (Table II.1). This corresponded very closely to dew formation. During January, February and December, which were very dry months in 1966 a possum without permanent water in its home range would have had to rely on obtaining water from its food.

Table II.1

Temporal and seasonal distribution of dew licking observations, and seasonal distribution of drinking observations made during the 1966 observation period.

Time	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	Total
before 24.00													
24.00									+				1
01.00							+						1
Dew 02.00				:	:		+	++		+			6
Licking 03.00				:			:				+:		4
04.00			:		++				++				5
Total			1	2	3		3	2	3	1	2		17
Drinking	1	1		2	2	1	1	1			1	1	11

: Dew licking on the ground
+ Dew licking in tree canopy

When drinking from a permanent water source such as a water trough, a possum lapped water for less than 0.5 min. On one occasion however when Alec had been inadvertently left in a trap for 2 to 3 days he made straight for the river 50 m away when released in broad daylight. He drank for 3 minutes 10 seconds (timed) only lifting his head twice to quickly look

round, before heading for his den.

II.7 RETCHING

Behaviour very similar to that described as regurgitation in other marsupials (see Barker, Brown and Calaby 1963 for summary) was observed eight times in the possum.

Typically the possum sat on its haunches and gave regular heaving contractions of the abdomen, with the front paws held together and moved up and down as the bouts of contractions occurred. When first seen I thought it was masturbation but the penis was not protruding and females performed exactly the same action. On one occasion I could distinctly hear a gagging sound. On another, a female regurgitated food into her mouth which she immediately swallowed without chewing. In the most violent retching session observed Alec was sitting on a horizontal branch with his haunches pressed hard against a vertical branch. As his abdomen heaved and his front paws worked up and down he gradually bent forward until he was lying on the branch with his head hanging and his mouth wide open, apparently absolutely exhausted.

Although regurgitation has been observed in many macropods it was irregular and probably infrequent, which led Barker, Brown and Calaby (1963) to conclude that it was not analogous to rumination in ruminants. In the possum six of the retching bouts followed feeding and one did not (one unknown), but because of its rare occurrence and because food was apparently regurgitated only the once, retching probably has not a definite role in the digestion of food. It appears to be more akin to a comfort movement in relation to indigestion. Five of the observations (3 male, 2 female) occurred during the courtship period, suggesting that possible tension due to social interaction may contribute to retching.

II.8 ALERT POSTURES

When alert a possum stares intently in a particular direction with its ears pricked and swivelled to point forward, but they may also be turned to the side or partially backwards, presumably to pick up sounds.

The most common arboreal alert position is the sitting alert in which

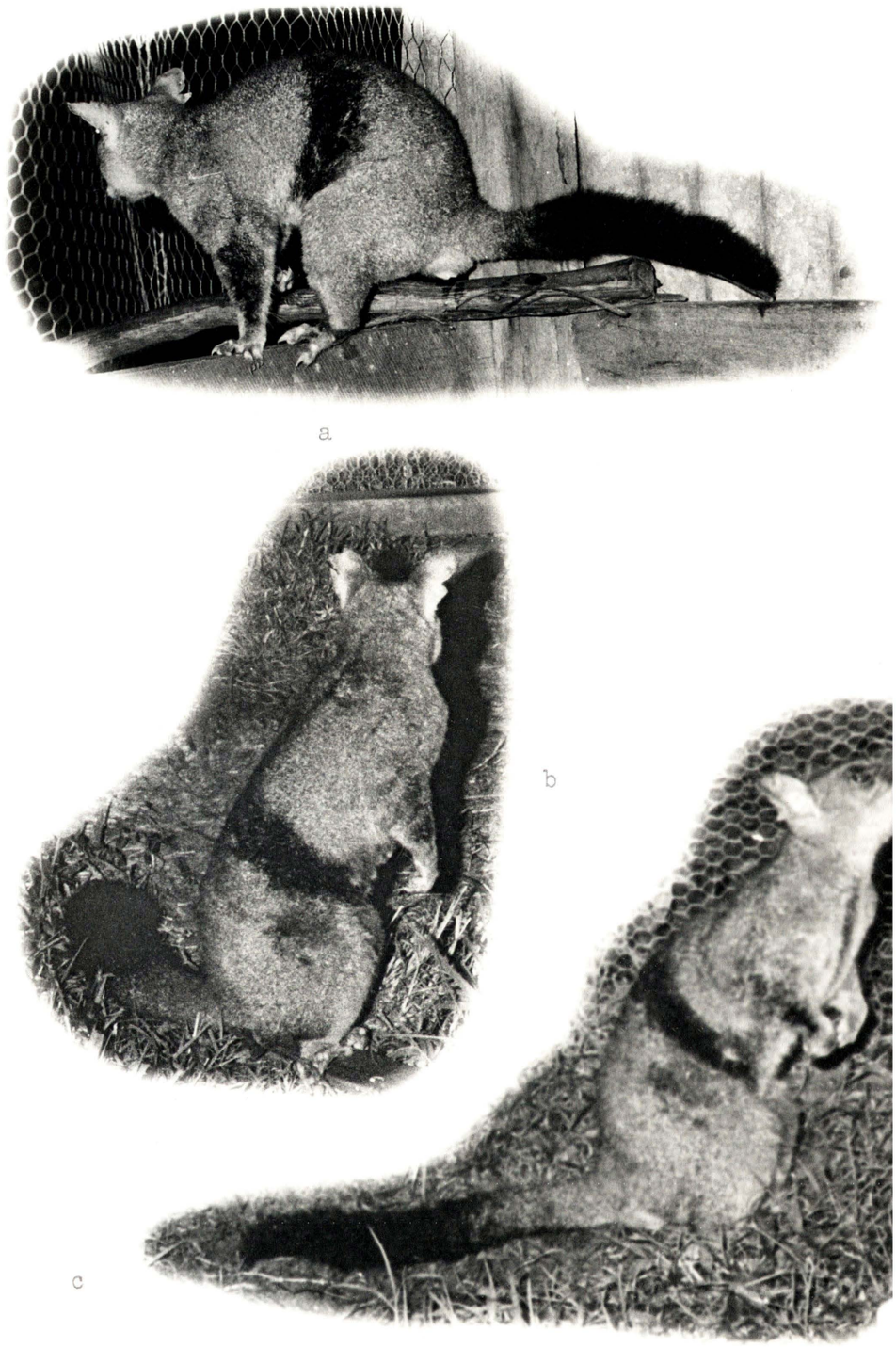


Figure II.15: Alert postures; a) standing alert; b) & c) upright or bipedal alert, note the down turned tail tip in c.

the head may be slightly thrust forward but the body remains relaxed (Fig. II.15b&c). This posture was adopted, for example, when a possum sitting on a low branch, up to 6m from the ground, peered down at another possum moving about on the ground below the tree, or as it 'watched' another climb about in the tree.

In the standing alert which occurred mainly on the ground, the possum stopped feeding or travelling and looked intently in one direction with ears pointed forward. Frequently one front paw remained suspended in mid air with the paw usually dangling relaxed and the fingers curled back (Fig. II.15a). This is identical to the 'indecision-alert' of Sminthopsis crassicaudata (Ewer 1968b) and very similar to that of the banded-anteater (Myrmecobius) (Calaby 1960), except that the anteater may also stamp its foot.

The upright alert is a bipedal posture in which the possum sits up on its hind feet, front paws tucked towards the lower midline of the body, tail held low and parallel to the ground, ears pricked, and peers intently into the night. This posture may vary from a relaxed forward hunch to a bolt upright stance (Fig. II.15b&c). It is usually held for 4-5 sec but may be held for up to 2 minutes. The tip of the tail turns down and in one bolt upright alert was clearly seen pressing hard against the ground, wobbling slightly from side to side under the pressure. Presumably this helped the balance of the possum, but it was not essential because a tailless male had no difficulty in maintaining a bolt upright posture. A female with a joey riding on her back can assume the bipedal alert unless the joey is forward over her shoulders, but she tends to do so rather less frequently. The upright alert is identical to the 'bipedal' stance, even to the tip of the tail pressed against the ground, of Sminthopsis crassicaud (Ewer 1968b). Similar postures have been described for Myrmecobius (Calaby 1960) and Dasycercus cristicaudata (Sorensson 1970).

Head-down and head-up alert postures occur when a possum is either descending or ascending a vertical tree trunk. In the first the possum stops and may lift the chest away from the trunk by bringing the spread

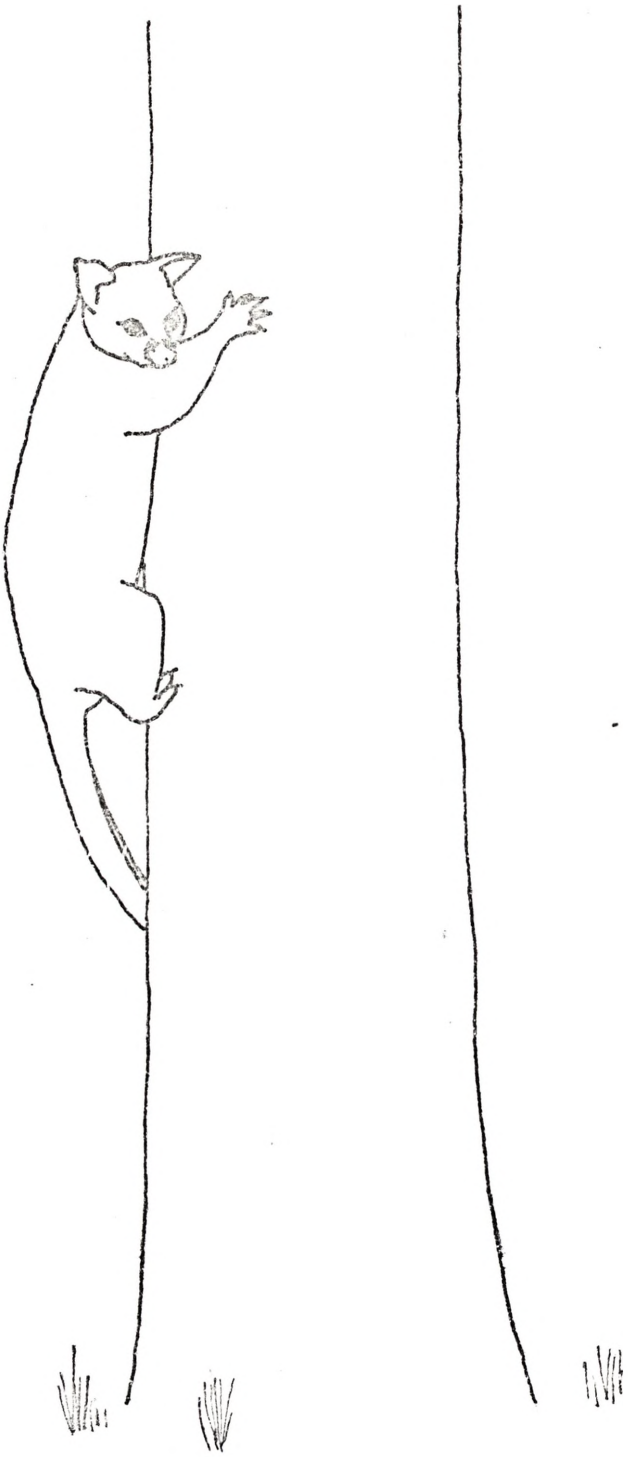


Figure II.16 : Head-up alert posture on a tree trunk following an alarm dash on the ground (traced from photograph).

Figure II.17: Flattened approach.

Figure II.18: A clump of the mistletoe (Amyema miquelii), the base of which (arrowed) is a favourite refuge for a disturbed possum.

eagled front legs closer together. Alice once maintained this more exaggerated position with the chest lifted off the trunk for 10 minutes. In the second posture the possum clings to the trunk as it turns its head to look to one side (Fig. II.16), a posture which it characteristically adopts after an alarm dash which is described later.

The flattened approach is used to make a very cautious approach to a strange object, such as a newly positioned trap. The body is pressed close to the ground, and leaning forward, as the possum crawls forward with its nose outstretched. The whole body is tensed and ready to draw back rapidly (Fig. II.17). A very similar posture to the flattened approach was once adopted by a female when startled whilst on the ground. She held it for only a split second before bounding away.

II.9 ALARM BEHAVIOUR

A number of types of behaviour indicated alarm. The mildest form was for a possum to climb higher into a tree when approached. A favourite position to move to in the tree when disturbed was the attachment position of a mistletoe clump, which meant that the dense foliage of the mistletoe was between the possum and myself (Fig. II.18). Several more apparent alarm behaviours were also seen.

Freeze:- when I approached with the spotlight trained on the possum it sometimes stopped moving to freeze in what ever position it happened to be in. If this was in the middle of crossing from one branch to another it held this position for about 2 min before beginning to shake with the muscular exertion of maintaining the position. Eventually it had to either draw back or complete the crossing. If sitting in a branch the possum sat stock still looking towards me, but not directly at me, with its ears swivelled back and slightly depressed. For a possum to freeze in this position it needed to be low off the ground and for me to have come on it suddenly. It was more likely to freeze with the spotlight trained on it.

Abandon tree:- When approached the usual behaviour of a possum in a tree was to climb higher. If, however, the tree was less than about

6m tall the possum left the tree. As I approached it sat and watched me, then if I came within 25 to 30m it rapidly descended the tree and bounded over to the nearest tall tree. Rarely did a possum climb to the top of the tree before descending to the ground, indicating that the possum knew the height of the tree without having to first climb to the top. Apparently a tree less than 6m offered insufficient security.

Long run:- A possum on the ground caught in the beam of the spotlight, and approached, usually reacted by climbing the nearest tree. Sometimes, on the other hand, a possum trotted away at a rapid pace to disappear over a rise in the ground. The distance covered was usually in excess of 50m and trees suitable as refuges were passed. Occasionally a long run was started by a possum coming down to the ground out of a tree, particularly if it had been sitting on a low branch less than 5m off the ground. The long run was started when I was still 100m or more from the possum, and the impression gained was of the possum running from me. However, in one long run made by Donald, when found on the periphery of his home range, he actually came towards me, from a distance of 90m, to pass within 20m of me to reach the core area of his home range. It is probable, therefore, that a long run is undertaken by a possum when disturbed on the periphery of its home range as it heads towards its core area. The distance made identification of individuals difficult, but all possums that were positively identified were adult males.

Alarm dash - a possum on the ground will suddenly bound away at high speed in an obvious alarm dash. The possum heads straight for a nearby tree and leaps onto its base to cling 1-2m off the ground as it peers in the direction from which the startling stimulus has come (Fig. II.16) The length of the dash may be as long as 20m but in the study area the distribution of trees meant that a possum was usually 5-10m from a tree. After a pause, varying in length from less than 0.1 min to about 1 min, in which it peered towards the source of alarm, the possum either jumped back to the ground (39/60 obs) or continued up the tree (21/60 obs). In 19 of the 108 alarm dashes recorded the possum stopped before reaching the

tree but usually close to its base.

Sudden loud noises such as a clap of thunder, honking of geese, the sudden drumming of horse's hooves, or my note book being dropped stimulated an alarm dash. Similarly any sudden movements such as a cow getting up from a prone position, or the sudden flap of a bush curlew's wing when the possum approached too close to the bird's nest on the ground, caused an alarm dash. Usually when I approached too close to a possum it trotted away, but if I approached a possum very cautiously it sometimes appeared to realise that I had come within its flight distance (Hediger 1950) and suddenly bounded away.

Possums also made alarm dashes in response to other possums. It occurred most commonly when two possums approached each other on the ground. When from 3 to 6m apart one or both of the possums sometimes made alarm dashes to nearby trees. If only one made the alarm dash it clung to the tree trunk watching the other possum until it had moved away. In one such meeting of two adult males one stood staring in the direction of the approaching male. When 5m apart both suddenly made alarm dashes away from each other. Alarm dashes were also stimulated by a screech 30-40m away and in at least two observations by a chatter.

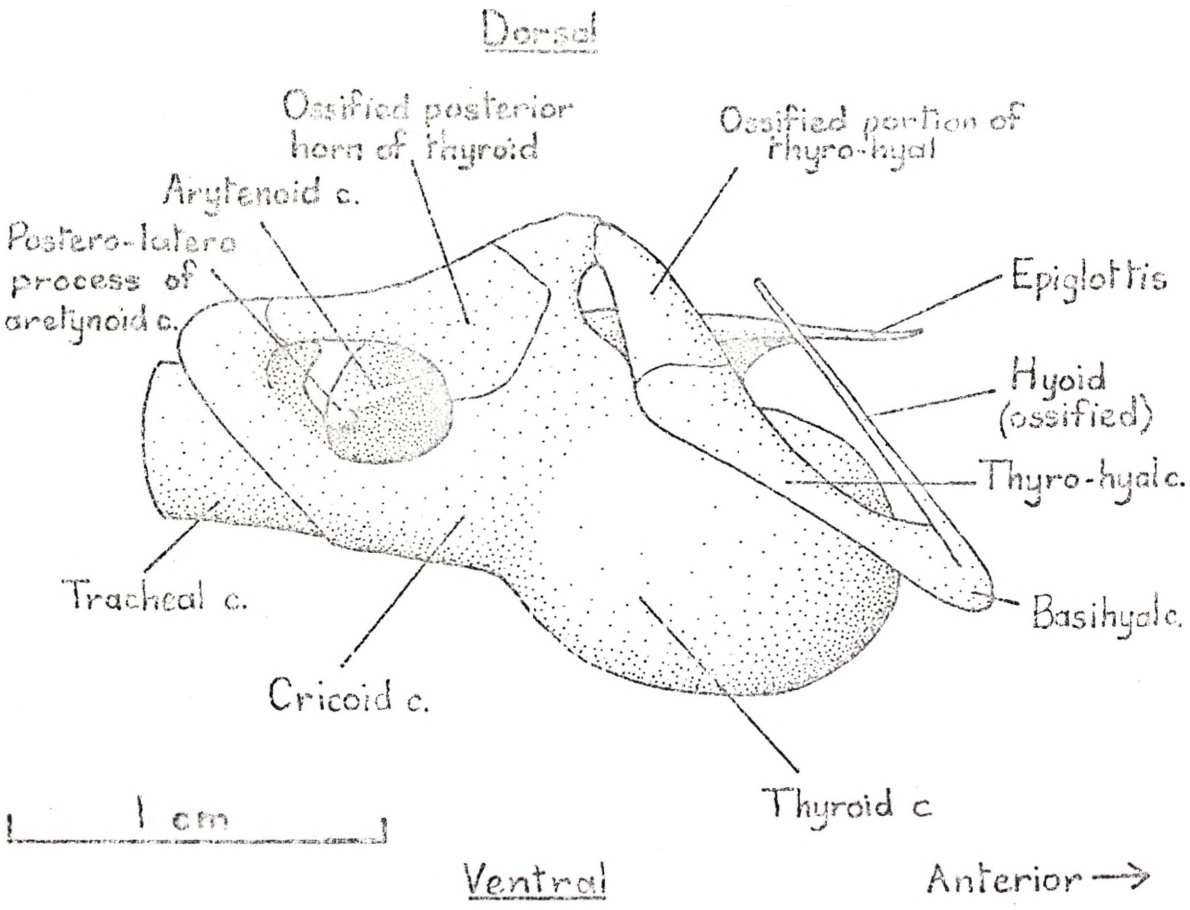


Figure III.1 : Lateral view of the laryngeal cartilages of an adult female Trichosurus vulpecula.

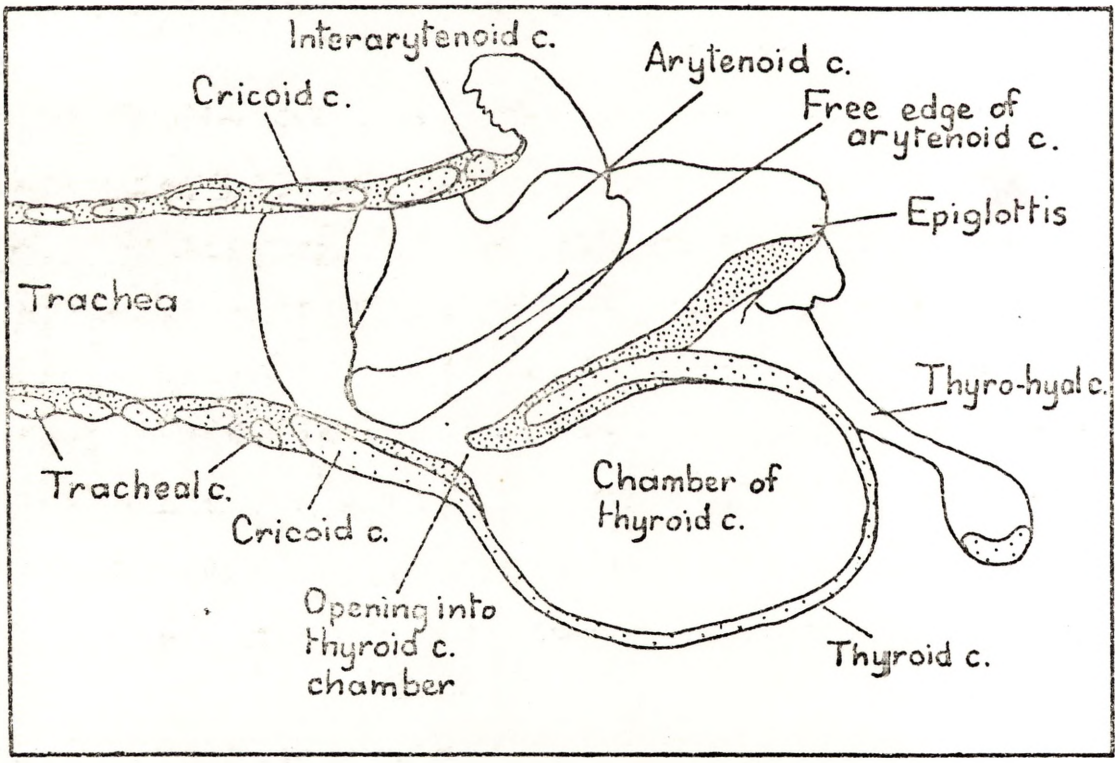


Figure III.3: Bisected larynx of T.vulpecula. Note free edge of arytenoid cartilage across main air passage of larynx, chamber of thyroid cartilage, and opening into chamber of thyroid cartilage with dorsal lip of soft tissue.

Appendix III

STRUCTURE OF LARYNX AND SOUND PRODUCTION

Negus (1949: 55-56) examined a number of marsupial larynges - kangaroo (Macropus sp.), bandicoot (Perameles), black wallaby (Macropus wallabatus), wombat (Phascolomys mitchelli), Tasmanian devil (Sarcophilus ursinus), vulpine phalanger (Trichosurus vulpecula), sombre phalanger (Trichosurus sp., probably the black colour variation of T.vulpecula). In both Trichosurus he found that the thyroid cartilage formed a rigid walled spherical chamber opening into the larynx, but no other marsupial had a similar chamber, and in fact it seems to be unique among mammals. Although many mammals have soft walled air sacs opening into the larynx, the only other mammal which Negus (1949 :57) found with a rigid walled chamber was the howler monkey (Mycetes), which has a dilated hyoid bone (see also Kelemen and Sade 1960). Negus suggested no function for the dilated thyroid cartilage of Trichosurus.

In Trichosurus the larynges of 4 specimens, 2 adult males and 2 adult females, were dissected. No sexual dimorphism was apparent, and one of the larynges is shown in Figures III.1-3. The thyroid cartilage forms a bulbous thin walled chamber opening into the floor of the larynx through a circular opening of approximately 1.5mm in diameter. The dorsal lip of the opening is composed of soft tissue possibly allowing the diameter of the opening to be varied (Fig. III.3). The arytenoid cartilages are large and can almost constrict the larynx. Large arytenoid cartilages and a corresponding lack of vocal folds are characteristic of marsupials. (Negus 1929 p.357).

The fricative sound produced by T.vulpecula sonograms show no evidence of a fundamental frequency or of harmonics, and is probably produced by air rushing between the free edges of the paired arytenoid cartilages. The irregular vertical striations seen on the sonograms of growls and chatters are assumed to be produced by the rather "sloppy" vibration of the large epiglottis.

No attempt was made to determine the function of the dilated thyroid

cartilage, but it is assumed to act as a resonator. It may be responsible for one of the formants seen on the sonograms and, since the wall of the chamber is rigid, one would expect little variation of the formant. Visual scanning of the sonograms indicates that the least variable of formants is the one at 1.0 Kh. Another possibility is that the chamber may function as a primary sound producer in the same way that a bottle can be made to produce a note by blowing across its opening. However, the apparent lack of a fundamental frequency in the sonograms suggests that the chamber is not acting as a primary sound producer.

Larynges of three other phalangerid marsupials - Pseudocheirus peregrinus, Petaurus norfolcencis, and Acrobates pygmaeus - were also examined briefly. None showed any structure resembling the dilated thyroid cartilage of T.vulpecula, but P.norfolcencis does have an unusually large spatulate-shaped hyoid cartilage. P.peregrinus which is about the same size as T.vulpecula has very soft vocalisations and it is suggested here that the louder calls of T.vulpecula, particularly the screech and chatter, are owing to the dilated thyroid cartilage. Another phalangerid which is similar to T.vulpecula both in size and in volume of its calls, is Petaurus australis. Its larynx has not been examined, but the enlarged hyoid cartilage of a smaller member of the same genus (P.norfolcencis) is an indication of the type of modification that could be expected - i.e. an enlarged hyoid being used to depress the floor of the buccal cavity and thus increase the volume of sound being emitted.

The presence of a probable resonating chamber in the larynx suggests that distance communication is important to T.vulpecula.

BIBLIOGRAPHY

Altmann, S.A. (1965). Sociobiology of rhesus monkeys. II. Stochastics of social communication. J. Theoret. Biol., 8: 490-522.

Andrew, R.J. (1963). The origin and evolution of the calls and facial expressions of the primates. Behaviour, 20: 1-109.

Anon. (1935). Carnivorous habits of the brush-tailed opossum (Trichosurus vulpecula). Aust. Zool. 8: 149.

Bailey, S.W. and Dunnet, G.M. (1960). The gaseous environment of the pouch young of the brush-tailed opossum, Trichosurus vulpecula Kerr. CSIRO Wildl. Res., 5: 149-151.

Baran, D. and Glickman, S.E. (1970). "Territorial marking" in the Mongolian gerbil: a study of sensory control and function. J. comp. physiol. Psychol., 71: 237-245.

Barker, S., Brown, G.D. and Calaby, J.H. (1963). Food regurgitation in the macropodidae. Aust. J. Sci., 25: 430-432.

Barnett, S.A. (1967). Instinct and Intelligence. The Science of Behaviour in Animals and Man. MacGibbon and Kee: London.

Batcheler, C.L., Darwin, J.H. and Pracy, L.T. (1967). Estimation of opossum (Trichosurus vulpecula) populations and results of poison trials from trapping data. N.Z. Jl Sci., 10: 97-114.

Bolliger, A. (1940). Trichosurus vulpecula as an experimental animal. Aust. J. Sci., 3: 59-61.

Bolliger, A. (1942). Spermatorrhoea in marsupials, with special reference to the action of sex hormones on spermatogenesis of Trichosurus vulpecula. J. Proc. R. Soc. N.S.W., 76: 86-92.

Bolliger, A. and Carrodus, A.L. (1938). Spermatorrhoea in Trichosurus vulpecula and other marsupials. Med. J. Aust., 12: 1118-1119.

Bolliger, A. and Hardy, M.H. (1944). The Sternal Integument of Trichosurus vulpecula. J. Proc. R. Soc. N.S.W., 78: 122-133.

Bolliger, A. and Whitten, W.K. (1948). The Paracloacal (Anal) Glands of Trichosurus vulpecula. J. Proc. Roy. Soc. N.S.W., 82: 36-43.

Borror, D.J. (1967). Songs of the yellowthroat. Living Bird, 6: 141-161.

Bossert, W.H. and Wilson, E.O. (1963). The analysis of olfactory communication among animals. J. Theoret. Biol., 5: 443-469.

Breeden, S. and Breeden, K. (1970). A natural history of Australia: 1. Tropical Queensland. Collins: Sydney and London.

Brown, J.L. (1964). The evolution of diversity in avian territorial systems. Wilson Bull., 76: 160-169.

Brown, L.E. (1966). Home range and movement of small mammals. Symp. zool. Soc. Lond., No. 18: 111-142.

Calaby, J.H. (1960). Observations on the banded ant-eater. Myrmecobius f. fasciatus Waterhouse (Marsupialia), with particular reference to its food habits. Proc. zool. Soc. Lond., 135: 183-207.

Calaby, J.H., Dimpel, H. and McTaggart Cowan, I. (1971). The mountain pigmy possum Burramys parvus Broom (Marsupialia) in the Kosciusko National Park, New South Wales. CSIRO Div. Wildl. Res. Tech. Pap. No. 23.

Caughley, G. (1964). Social organization and daily activity of the red kingaroo and the grey kangaroo. J. Mammal., 45: 429-436.

Caughley, G. and Kean, R.I. (1964). Sex ratios in marsupial pouch young. Nature, Lond., 204: 491.

Charles-Dominique, P. (1972). Ecologie et vie sociale de Galago demidovii (Fischer 1808, Prosimii). Beih. Z. Tierpsychol., 9: 7-41.

Cherry, C. (1957). On human communication. A review, a survey and a criticism. New York. John Wiley.

Crawley, M.C. (1970). Longevity of Australian brush-tailed opossums (Trichosurus vulpecula) in indigenous forest in New Zealand. N.Z. Jl Sci., 13: 348-351.

Crawley, M.C. (1973). A live-trapping study of Australian brush-tailed possum, Trichosurus vulpecula (Kerr), in the Orongorongo Valley, Wellington, New Zealand. Aust. J. Zool., 21: 75-90.

Crook, J.H. (1970). The Socio-ecology of Primates. In Crook, J.H. (ed.). Social Behaviour in Birds and Mammals. Academic Press: London. pp. 103-166.

Crook, J.H. and Gartlan, J.S. (1966). Evolution of primate societies. Nature, Lond., 210: 1200-1203.

Dagg, A.I. and Windsor, D.E. (1971). Olfactory discrimination limits in gerbils. Can. J. Zool., 49: 283-285.

Dawson, T.J. and Hulbert, A.J. (1969). Standard energy metabolism of marsupials. Nature, Lond., 221: 383.

Dimpel, H. and Calaby, J.H. (1972). Further observations on the mountain pigmy possum (Burramys parvus). Victoria Nat., 89: 101-106.

Dixon, A.K. and Mackintosh, J.H. (1971). Effects of female urine upon the social behaviour of adult male mice. Anim. Behav., 19: 138-140.

Dunford, C. (1970). Behavioral aspects of spatial organization in the chipmunk, Tamias striatus. Behaviour, 36: 215-231.

Dunnet, G.M. (1956). A live-trapping study of the brush-tailed possum Trichosurus vulpecula Kerr (Marsupialia). CSIRO Wildl. Res., 1: 1-18.

Dunnet, G.M. (1964). A field study of local populations of the brush-tailed possum, Trichosurus vulpecula, in eastern Australia. Proc. zool. Soc. Lond., 142: 665-695.

Eisenberg, J.F., Muckenhirn, N.A., and Rudran, R. (1972). The relation between ecology and social structure in primates. Science, 176: 863-874.

Elton, C.S. (1958). The Ecology of Invasions by Animals and Plants. Wiley: New York.

Epple, Gisela (1971). Discrimination of the odor of males and females by the marmoset Saguinus fuscicollis ssp.[1] Proc. 3rd Int. Congr. Primat. Zurich 1970, 3: 166-171.

Estes, R.D. (1974). Social organization of the African bovids. In Ungulate Behaviour and its Relation to Management: Proceedings of the Calgary Symposium, 1971. (Ed. by V. Geist). Morges: I.U.C.N.

Everist, S. (1974). Poisonous Plants of Australia. Angus and Robertson: Sydney.

Ewer, R.F. (1968a). Ethology of Mammals. London: Logos Press.

Ewer, R.F. (1968b). A preliminary survey of the behaviour in captivity of the dasyurid marsupial, Sminthopsis crassicaudata (Gould). Z. Tierpsychol., 25: 319-365.

Fant, C.G.M. (1956). On the predictability of formant levels and spectrum envelopes from formant frequencies. Reprinted in Lehiste, I. (1967). Readings in Acoustic Phonetics. The M.I.T. Press: Cambridge, Massachusetts. pp. 44-56.

Finlayson, H.H. (1963). The brush-tailed opossum of Kangaroo Island, South Australia. Trans. R. Soc. S. Aust., 87: 17-22.

Fisler, G.F. (1969). Mammalian organizational systems. Contr. Sci., No. 167: 1-32.

Fleay, D. (1942). The numbat in Victoria. Victoria Nat., 59: 3-7.

Fleay, D. (1947). Gliders of the Gum Trees. Melbourne: Bread and Cheese Club.

Frith, H.J. and Calaby, J.H. (1969). Kangaroos. F.W. Cheshire: Melbourne.

Gardner, C.A. and Bennetts, H.W. (1956). The toxic plants of Western Australia. Western Australian Newspapers Ltd.: Perth.

Giles, R.H. (1969). Wildlife Management Techniques. 3rd ed. The Wildlife Society: Washington.

Gilmore, D.P. (1965). Food of the opossum Trichosurus vulpecula in pastoral areas of Banks Peninsula, Canterbury. Proc. N.Z. Ecol. Soc., 12: 10-13.

Gilmore, D.P. (1967). Foods of the Australian opossum (Trichosurus vulpecula Kerr) on Banks Peninsula, Canterbury and a comparison with other selected areas. N.Z. Jl Sci., 10: 235-279.

Gilmore, D.P. (1969). Seasonal reproductive periodicity in the male Australian brush-tailed possum. (Trichosurus vulpecula). J. Zool., Lond., 157: 75-98.

Grant, E.C., Mackintosh, J.H. and Lerwill, C.J. (1970). The effect of a visual stimulus on the agonistic behaviour of the golden hamster. Z. Tierpsychol., 27: 73-77.

Grant, T.R. (1973). Dominance and association among members of a captive and free-ranging group of grey kangaroos. (Macropus giganteus). Anim. Behav., 21: 449-456.

Grau, G.A., Sanderson, G.C., and Rogers, J.P. (1970). Age determination of racoons. J. Wildl. Mgmt., 34: 364-372.

Hall, K.R.L. (1965). Behaviour and ecology of the wild Patas monkey, Erythrocebus patas, in Uganda. J. Zool. Lond., 148: 15-87.

Hartman, C.G. (1952). Possums. Austin: Univ. Texas Press.

Harvie, A.E. (1973). Diet of the opossum (Trichosurus vulpecula Kerr) on farmland northeast of Waverley, New Zealand. Proc. N.Z. ecol. Soc., 20: 48-52.

Hediger, H. (1950). Wild Animals in Captivity. Butterworth: London.

Heinsohn, G.E. (1966). Ecology and reproduction of the Tasmanian bandicoots (Perameles gunni and Isoodon obesulus). Univ. California Publs Zool., 80: 1-107.

Hinde, R.A. and Rowell, T.E. (1962). Communication by postures and facial expressions in the rhesus monkey (Macaca mulatta). Proc. zool. Soc. Lond., 138: 1-21.

Hope, R.M. (1972). Observations on the sex ratio and the position of the lactating mammary gland in the brush-tailed possum, Trichosurus vulpecula (Kerr) (Marsupialia). Aust. J. Zool., 20: 131-137.

Hughes, R.L. and Rodger, J.C. (1971). Studies on the vaginal mucus of the marsupial Trichosurus vulpecula. Aust. J. Zool., 19: 19-33.

Jewell, P.A. (1966). The concept of home range in mammals. Symp. zool. Soc. Lond., No. 18: 85-109.

Jolly, A. (1966). Lemur Behaviour. The University of Chicago Press: Chicago and London.

Jolly, J.N. (1973). Movements and social behaviour of the opossum, Trichosurus vulpecula Kerr, in a mixed scrub, bush and pasture habitat. Mauri Ora, 1: 65-71.

Jones, F.W. (1921). On the habits of Trichosurus vulpecula. J. Mammal., 2: 187-193.

Jones, F.W. (1924). The Mammals of South Australia. Government Printer: Adelaide.

Kalkowski, W. (1967). Olfactory Bases of Social Orientation in the White Mouse. Folia Biol. (Cracow), 15: 69-87.

Kalmus, H. (1955). The discrimination by the nose of the dog of individual human odours and in particular the odours of twins. Br. J. Anim. Ecol., 3: 25-31.

Kaufmann, J.H. (1962). Ecology and social behaviour of the coati, Nasua narica on Barro Colorado Island, Panama. Uni. Calif. Publs. zool., 60: 95-222.

Kaufmann, J.H. (1974). Social ethology of the whiptail wallaby, Macropus parryi, in northeastern New South Wales. Anim. Behav., 22: 281-369.

Kaufmann, J.H. and Kaufmann, A. (1963). Some comments on the relationships between field and laboratory studies of behaviour, with special reference to coatis. Anim. Behav., 11: 464-469.

Kean, R.I. (1959). Bionomics of the brush-tailed opossum Trichosurus vulpecula in New Zealand. Nature, Lond., 184: 1388-1389.

Kean, R.I. (1967). Behaviour and territorialism in Trichosurus vulpecula (Marsupialia). Proc. N.Z. ecol. Soc., 14: 71-78.

Kean, R.I. (1971). Selection for melanism and for low reproductive rate in Trichosurus vulpecula (Marsupialia). Proc. N.Z. ecol. Soc., 18: 42-47.

Kean, R.I., Marryatt, R.G., and Carroll, A.L.K. (1964). The female urogenital system of Trichosurus vulpecula (Marsupialia). Aust. J. Zool., 12: 18-41.

Kelemen, G. and Sade, J. (1960). The vocal organ of the howling monkey (Alouatta palliata). J. Morph., 107: 123-140.

King, J.A. (1955). Social behaviour, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hill of South Dakota. Contr. Lab. vertebr. Biol. Univ. Mich., 67: 1-123.

Kingsmill, E. (1962). An investigation of criteria for estimating age in the marsupials Trichosurus vulpecula Kerr and Perameles nasuta Geoffroy. Aust. J. Zool., 10: 597-616.

Kirsch, J.A.W. (1968). Prodromus of the comparative serology of marsupialia. Nature, Lond., 217: 418-420.

Kleiman, D.G. (1966). Scent marking in the canidae. Symp. zool. Soc. Lond., 18: 167-177.

Kummer, H. (1968). Social Organization of Hamadryas Baboons. The University of Chicago Press: Chicago and London.

Kummer, H. (1971). Immediate causes of primate social structures. Proc. 3rd Int. Congr. Primat., Zurich 1970, Vol. 3: 1-11. (Karger, Basel).

Ladefoged, P. and Broadbent, D.E. (1957). Information conveyed by vowels. Reprinted in Lehiste, I. (1967). Readings in Acoustic Phonetics. The M.I.T. Press: Cambridge, Massachusetts. pp. 326-332.

van Lawick-Goodall, J. (1968). The Behaviour of Free-living Chimpanzees in the Gombe Stream Area. Anim. Behav. Monogr., 1: 161-311.

Lay, D.W. (1942). Ecology of the opossum in eastern Texas. J. Mammal., 23: 147-159.

Leeper, G.W. (1970). The Australian Environment. 4th ed. Melbourne University Press: Carlton.

Leyhausen, P. (1965). The communal organization of solitary mammals. Symp. zool. Soc. Lond., 14: 249-263.

Leyhausen, P. (1971). Dominance and territoriality as complemented in mammalian social structure. In Behaviour and Environment. Ed. Esser, A.H. Plenum Press: New York, London. pp. 22-33.

Lockie, J.D. (1966). Territory in small carnivores. Symp. zool. Soc. Lond., 18: 143-165.

Lyne, A.G., Pilton, P.E., and Sharman, G.B. (1959). Oestrous cycle, gestation period and parturition in the marsupial Trichosurus vulpecula. Nature, Lond., 183: 622-623.

Lyne, A.G. and Verhagen, A.M.W. (1957). Growth of the marsupial Trichosurus vulpecula and a comparison with some higher mammals. Growth, 21: 167-195.

MacLean, L. (1967). A note on the longevity and territoriality of Trichosurus vulpecula (Kerr) in the wild. CSIRO Wildl. Res., 12: 81-82.

McManus, J.J. (1970). Behavior of captive opossums, Didelphis marsupialis virginiana. Am. Midl. Nat., 84: 144-169.

McNally, J. (1955). Damage to Victorian exotic pine plantations by native animals. Aust. For., 19: 87-99.

Marler, P. (1965). Communication in monkeys and apes. In Primate Behaviour. Ed. I. De Vore. Holt, Rinehart and Winston: New York. pp. 544-584.

Marler, P. (1967). Animal communication signals. Science, 157: 769-774.

Marlow, B.J. (1961). Reproductive behaviour of the marsupial mouse, Antechinus flavipes (Waterhouse) (Marsupialia) and the development of the pouch young. Aust. J. Zool., 9: 203-218.

Marlow, B.J. (1962). Marsupials of Australia. The Jacaranda Press: Brisbane.

Marples, T.G. (1973). Studies on the marsupial glider Schoinobates volans (Kerr). IV. Feeding biology. Aust. J. Zool., 21: 213-216.

Marsh, M. (1967). Ring-tailed possums. Aust. Natur. His., 15: 294-297.

Martin, R.D. (1972). A preliminary field-study of the lesser mouse lemur (Microcebus murinus J.F. Miller 1777). Beih. Z. Tierpsychol., 9: 43-89.

Martinsen, D.L. (1968). Temporal patterns in the home ranges of chipmunks (Eutamias). J. Mammal., 49: 83-91.

Mason, R. (1958). Foods of the Australian opossum (Trichosurus vulpecula, Kerr) in New Zealand indegenous forest in the Orongorongo Valley, Wellington. N.Z. Jl Sci., 1: 590-613.

Matthews, L.H. (1969). The Life of Mammals. Vol. I. Weidenfeld and Nicholson: London.

Michael, R.P. and Keverne, E.B. (1968). Pheromones in the communication of sexual status in primates. Nature, Lond., 218: 746-749.

Michael, R.P., Keverne, E.B., and Bonsall, R.W. (1971). Pheromones: Isolation of male sex attractants from a female primate. Science, 172: 964-966.

Morris. D. (1956). Feather postures of birds and the problems of the origins of social signals. Behaviour, 9: 75-113.

Muller-Schwarze, D. (1971). Pheromones in Black-tailed Deer (Odocoileus hemionus columbianus). Anim. Behav., 19: 141-152.

Myers, K. and Poole, W.E. (1963). A study of the biology of the wild rabbit, Oryctolagus cuniculus (L.), in confined populations. V. Population dynamics. CSIRO Wildl. Res., 8: 166-203.

Mykytowycz, R. (1961). Social behaviour of an experimental colony of wild rabbits, Oryctolagus cuniculus (L.). IV. Conclusion: Outbreak of myxomatosis, third breeding season and starvation. CSIRO Wildl. Res., 6: 142-155.

Mykytowycz, R. (1962). Territorial function of chin gland secretion in the rabbit, Oryctolagus cuniculus (L.). Nature, Lond., 193: 799.

Mykytowycz, R. (1965). Further observations on the territorial function and histology of the submandibular cutaneous (chin) glands in the rabbit, Oryctolagus cuniculus (L.). Anim. Behav., 13: 400-412.

Mykytowycz, R. and Hesterman, E.R. (1970). The behaviour of captive wild rabbits, Oryctolagus cuniculus (L.) in response to strange dung-hills. forma functio, 2: 1-12.

Mykytowycz, R. and Ward, M.M. (1971). Some reactions of nestlings of the wild rabbit, Oryctolagus cuniculus (L.), when exposed to natural rabbit odours. forma functio, 4: 137-148.

Nagel, U. (1971). Social organization in a baboon hybrid zone. Proc. 3rd int. Congr. Primat., Zurich 1970, 3: 48-57 (Karger, Basel).

Negus, V.E. (1929). The Mechnaism of the Larynx. W.M. Heinemann (Medical Books) Ltd.: London.

Negus, V.E. (1949). The Comparative Anatomy and Physiology of the Larynx. Hafner Publishing Co.: New York, London.

Owen, W.H. and Thomson, J.A. (1965). Notes on the comparative ecology of the common brushtail and mountain possums in eastern Australia. Victoria Nat., 82: 216-217.

Pekelharing, C.J. (1970). Cementum deposition as an age indicator in the brush-tailed possum, Trichosurus vulpecula Kerr (Marsupialia). Aust. J. Zool., 18: 71-76.

Pilton, P.E. and Sharman, G.B. (1962). Reproduction in the marsupial Trichosurus vulpecula. J. Endocr., 25: 119-136.

Pitelka, F.A. (1959). Numbers, breeding schedule, and territoriality in pectoral sandpipers of northern Alaska. Condor, 61: 233-264.

Pracy, L.T. (1962). Introduction and liberation of the opossum (Trichosurus vulpecula) into New Zealand. Inf. Ser. N.Z. Forest Serv., No. 45: 1-28.

Pracy, L.T. and Kean, R.I. (1969). The opossum in New Zealand. Habits and trapping. N.Z. Forest Service Publ. Item No. 40: 1-52.

Ralls, K. (1971). Mammalian scent marking. Science, 171: 443-449.

Randall, R.H. (1951). An Introduction to Acoustics. Addison-Wesley Press Inc.: Cambridge Mass.

Reynolds, H.C. (1952). Studies on reproduction in the opossum (Didelphis virginiana virginiana). Univ. Calif. Publs. Zool., 52: 223-284.

Ride, W.D.L. (1970). A Guide to the Native Mammals of Australia. Oxford University Press: Melbourne.

Ridpath, P. (1967). Possum Moods. Ure Smith Pty. Ltd.: Sydney.

Robinette, W.L., Jones, D.A., Rogers, G. and Gashwiler, J.S. (1957). Notes on tooth development and wear for Rocky Mountain Mule Deer. J. Wild. Mgmt., 21: 134-153.

Rohlf, F.J. and Sokal, R.R. (1969). Statistical Tables. San Francisco: W.H. Freeman and Company.

Ropartz, P. (1968). Olfaction et comportment social chez les rongeurs. Mammalia, 32: 550-569.

Rowell, T.E. (1966). Forest living baboons in Uganda. J. Zool. Lond., 149: 344-364.

Rowell, T.E. (1967). A quantitative comparison of the behaviour of a wild and a caged baboon group. Anim. Behav., 15: 499-509.

Rowell, T.E. and Hinde, R.A. (1962). Vocal communication by the rhesus monkey (Macaca mulatta). Proc. zool. Soc. Lond., 138: 279-294.

Rowley, I. (1956). Individual marking of the rabbit, Oryctolagus cuniculus (L.). CSIRO Wildl. Res., 1: 40-44.

Russell, E.M. (1970a). Agonistic interactions in the red kangaroo, (Megaleia rufa). J. Mammal., 51: 80-88.

Russell, E.M. (1970b). Observations on the behaviour of the red kangaroo (Megaleia rufa) in captivity. Z. Tierpsychol., 27: 385-404.

Russell, E.M. (1973). Mother-young relations and early behavioural development in the marsupials Macropus eugenii and Megaleia rufa. Z. Tierpsychol., 33: 163-203.

Ryel, L.A., Fay, L.D. and van Etten, R.C. (1961). Validity of age determination in Michigan deer. Pap. Mich. Acad. Sci., 46: 389-316.

Sault, T. and Taylor, M. (1974). Fluffy gliders abroad in daylight. Victoria Nat., 91: 203-204.

Schaller, G.B. (1963). The Mountain Gorilla, Ecology and Behaviour. The University of Chicago Press: Chicago.

Schultze-Westrum, T. (1965). Innerartliche verständigung durch Düfte beim Gleitbeutler Petaurus breviceps papuanus Thomas (Marsupialia, Phalangeridae). Z. vergl. Physiol., 50: 151-220.

Sharman, G.B. (1962). The initiation and maintenance of lactation in the marsupial Trichosurus vulpecula. J. Endocr., 25: 375-385.

Sharman, G.B. and Calaby, J.H. (1964). Reproductive behaviour in the red kangaroo, Megaleia rufa, in captivity. CSIRO Wildl. Res., 9: 58-85.

Sharman, G.B., Calaby, J.H. and Poole, W.E. (1966). Patterns of reproduction in female diprotodont marsupials. Symp. zool. Soc. Lond., No. 15: 205-232.

Smith, C.C. (1968). The adaptive nature of social organization in the genus of tree squirrels Tamiasciurus. Ecol. Monogr., 38: 31-63.

Smith, M.J., Brown, B.K., and Frith, H.J. (1969). Breeding of the brush-tailed possum, Trichosurus vulpecula (Kerr), in New South Wales. CSIRO Wildl. Res., 14: 181-193.

Smith, R.F.C. (1969). Studies on the marsupial glider, Schoinobates volans (Kerr). 1. Reproduction. Aust. J. Zool., 17: 625-636.

Smith, W.J. (1965). Message, meaning, and context in ethology. Am. Nat., XCIX: 405-409.

Snedecor, G.W. and Cochran, W.G. (1967). Statistical Methods. Sixth ed. Iowa State University Press: Iowa.

Sokal, R.R. and Rohlf, F.J. (1969). Biometry. W.H. Freeman and Company: San Francisco.

Sorenson, M.W. (1970). Observations on the behaviour of Dasycercus cristicauda and Dasyuroides byrnei in captivity. J. Mammal., 51: 123-130.

Southern, H.N. (1948). Sexual and aggressive behaviour in the wild rabbit. Behaviour, 1: 173-194.

Stevens, K.N. and House, A.S. (1961). An acoustical theory of vowel production and some of its implications. Reprinted in Lehiste, I. (1967). Readings in Acoustic Phonetics. The M.I.T. Press: Cambridge, Massachusetts. pp. 88-90.

Stickel, L.F. (1954). A comparison of certain methods of measuring ranges of small mammals. J. Mammal., 35: 1-15.

Stodard, E. (1965). Management and behaviour of breeding groups of the marsupial Perameles nasuta Geoffroy in captivity. Aust. J. Zool., 14: 611-623.

Stodart, E. (1966). Observations on the behaviour of the marsupial Bettongia lesuerri (Quoy & Gaimard) in an enclosure. CSIRO Wildl. Res., 11: 91-99.

Struhsaker, T.T. (1967a). Auditory communication among vervet monkeys, (Cercopithecus aethiops). In: Altman, S.A. Social Communication among Primates. University of Chicago Press: Chicago. pp. 281-324.

Struhsaker, T.T. (1967b). Behaviour of vervet monkeys (Cercopithecus aethiops). Univ. Calif. Publs. zool., 82: 1-64.

Struhsaker, T.T. (1969). Correlates of ecology and social organization among African Cercopithecines. Folia primatol., 11: 80-118.

Taylor, J.C. (1966). Home range and agonistic behaviour in the grey squirrel. Symp. zool. Soc. Lond., No. 18: 229-235.

Taylor, R.H. and Magnussen, W.B. (1965). Immobilising live-trapped opossums with succinylcholine chloride. N.Z. Jl Sci., 8: 531-536.

Thomson, J.A. and Owen, W.H.(1964). A field study of the Australian ringtail possum Pseudocheirus peregrinus (Marsupialia: Phalangeridae). Ecol. Monogr., 34: 27-52.

Thomson, J.A. and Pears, F.N. (1962). The functions of the anal glands of the brushtail possum. Victoria Nat., 78: 306-308.

Troughton, E. (1962). Furred Animals of Australia. Angus and Robertson: Sydney.

Tyndale-Biscoe, C.H. (1955). Observations on the reproduction and ecology of the brush-tailed possum, Trichosurus vulpecula Kerr (Marsupialia), in New Zealand. Aust. J. Zool., 3: 162-184.

Tyndale-Biscoe, C.H. (1960). The possum in New Zealand. Aust. Mus. Mag., 13: 235-238.

Tyndale-Biscoe, C.H. and Smith, R.F.C. (1969). Studies on the marsupial glider, Schoinobates volans (Kerr). II. Population structure and regulatory mechanisms. J. Anim. Ecol., 38: 637-650.

Wakefield, N.A. (1970). Notes on the glider-possum, Petaurus australis (Phalangeridae, Marsupialia). Victoria Nat., 87: 221-236.

Walls, G.L. (1963). The Vertebrate Eye and its Adaptive Radiation. Hafner Publishing Co.: New York.

Walker, E.P. (1964). Mammals of the World. I. John Hopkins Press: Baltimore.

Ward, G.D. (1972). Techniques for tracking opossums (Trichosurus vulpecula) by radio telemetry in New Zealand lowland forest. N.Z. Jl Sci., 15: 628-636.

Winter, J.W. (1963). Observation on a population of the brush-tail opossum. Unpub. M.Sc. thesis, University of Otago, New Zealand.

Winter, J.W. (1966). Bird predation by the Australian Marsupial Squirrel Glider. J. Mammal., 47: 530.

Wodzicki, K.A. (1950). Introduced mammals of New Zealand. Bull. N.Z. Dep. Scient. Ind. Res., No. 98: 1-255.

Wolfe, J.L. (1966). Agonistic behaviour and dominance relationships of the eastern chipmunk, Tamias straitus. Am. Midl. Nat., 76: 190-200.